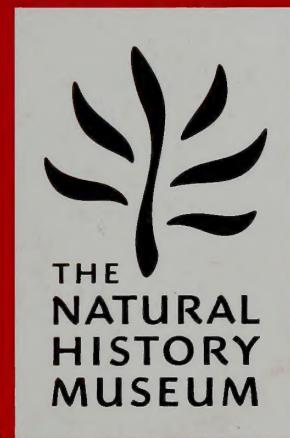
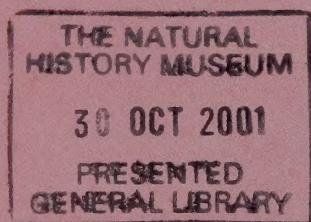


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## Zoology Series



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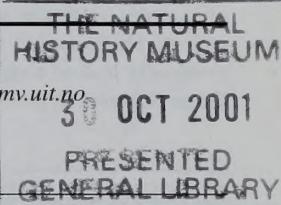
# Type material of Stegocephalidae Dana, 1855 (Crustacea, Amphipoda) in the collections of The Natural History Museum, London, including the description of seven new species

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## CONTENTS

Synopsis .....	109
Introduction .....	109
Material and methods .....	110
Systematics .....	110
<i>Andaniexis australis</i> K.H. Barnard, 1932 .....	110
<i>Andaniexis americana</i> sp.nov. ....	111
<i>Andaniexis gloriosa</i> sp.nov. ....	113
<i>Andaniexis pelagica</i> sp.nov. ....	113
<i>Andaniopsis africana</i> sp.nov. ....	117
<i>Bathystegocephalus globosus</i> (Walker, 1909) ....	119
<i>Phippisia gibbosa</i> (Sars, 1883) ....	120
<i>Phippiella rostrata</i> K.H. Barnard, 1932 .....	121
<i>Stegocephaloides attingens</i> K.H. Barnard, 1932 .....	124
<i>Stegocephaloides australis</i> K.H. Barnard, 1916 .....	127
<i>Stegocephaloides calypsonis</i> sp.nov. ....	129
<i>Stegocephaloides boxshalli</i> sp.nov. ....	129
<i>Stegocephaloides ledoyerii</i> sp.nov. ....	131
Discussion .....	135
References .....	135

**SYNOPSIS.** Six species belonging to the amphipod family Stegocephalidae Dana, 1855 (Crustacea) are redescribed and figured. Seven new species are also described: *Andaniexis americana* sp.nov., *A. gloriosa* sp.nov. and *A. pelagica* sp.nov., *Andaniopsis africana* sp.nov., *Stegocephaloides boxshalli* sp.nov., *S. calypsonis* sp.nov. and *S. ledoyerii* sp.nov. The type material of *Stegocephaloides attingens* K.H. Barnard 1916 comprises two species, *S. attingens* and *S. boxshalli* sp.nov. *Stegocephaloides calypsonis* is formally described for the first time, but was originally described in the PhD thesis of Anton Galan (1984).

## INTRODUCTION

Many species in the amphipod family Stegocephalidae Dana, 1855 were described at the end of the 19<sup>th</sup> or the beginning of the 20<sup>th</sup> century. These descriptions usually took the form of a limited descriptive text accompanied by very few figures, typically showing only one or two diagnostic characters. Very few of these species have been later redescribed in any detail, and when they have, the description was usually based on new material without any reference to the type material (e.g. Barnard, 1962, 1964; Ledoyer, 1986; all referring to *Andaniexis australis* K.H.Barnard 1932). Con-

sequently, for a number of stegocephalid species, there is considerable confusion in terms of morphology, generic and specific status.

The vast collections of The Natural History Museum in London (UK) include type material of nine stegocephalid species, none of which has ever been redescribed from the type material. Three of these species belong to the genus *Andaniotes* Stebbing, 1897; which have recently been dealt with elsewhere (Berge, 2001a.). In the present paper, the type material of six species is redescribed and figured: *Andaniexis australis* K.H.Barnard, 1932, *Bathystegocephalus globosus* (Walker, 1909), *Phippisia gibbosa* (Sars, 1883), *Phippiella rostrata* K.H.Barnard, 1932, *Stegocephaloides attingens* K.H.Barnard, 1916 and *S. australis* K.H.Barnard, 1916. In addition

to these six species, one, *Stegocephaloïdes calypsonis* sp.nov., is formally described for the first time, although it was first recognized by Anton Galan in his unpublished Ph.D. thesis (1984).

As a 'spin-off' effect of describing some of the above mentioned species, six further new species are described: *Andaniexis americana*, *A. gloriosa* and *A. pelagica*, *Andaniopsis africana*, *Stegocephaloïdes boxshalli* and *S. ledoyerii*. All these species have previously been assigned to one of the six redescribed species.

The phylogenetic relationships and generic status of the species described herein are not discussed in the present paper, which is one of a series (together with Berge & Vader 1997 a-d) that will collectively revise all the genera and species in the family, and eventually lead to a phylogenetic analysis of the Stegocephalidae (Berge & Vader, in press).

## MATERIAL AND METHODS

The present study is based primarily on material from the collections of the Natural History Museum in London, UK (BMNH). Additional material has been borrowed from the American Museum of Natural History, New York (AMNH) and the South African Museum, Cape Town (SAM).

All dissected appendages were mounted in polyvinyl-lactophenol and stained with rose-bengal. Figures of these appendages were made using a Leica compound microscope, while the habitus-drawings were made using a Leica dissecting microscope. Mature and immature females were distinguished from males by the presence of oostegites.

Scales on figures are all 0.1 mm. Classification of setae and setae-groups follow the scheme of Berge (2001b).

**Symbols:** A1–2: Antenna 1–2; EP3: Epimeral plate 3; L: Labium; LBR: Labrum; LMND: Left mandible; MX1: Maxilla 1; MX2: Maxilla 2; MXP: Maxilliped; P1–7: Pereopods 1–7; PLP: palp; RMND: Right mandible; T: Telson; U1–3: Uropod 1–3.

## SYSTEMATICS

Family STEGOCEPHALIDAE Dana, 1855  
Type genus: *STEGOCEPHALUS* Krøyer, 1842

### *Andaniexis* Stebbing, 1906

*Andania* Boeck, 1871: 128. Homonym, Lepidoptera  
*Andaniexis* Stebbing, 1906: 94

### *Andaniexis australis* K.H.Barnard, 1932

(Figs 1–3)

*Andaniexis australis* K.H.Barnard, 1932: 76  
Non *A. australis* Barnard 1964 (= *A. pelagica* sp.nov.)  
Non *A. australis* Barnard 1962 (= *A. americana* sp.nov.)  
Non *A. australis* Ledoyer 1986 (= *A. gloriosa* sp.nov.)

MATERIAL EXAMINED. Syntypes 4 females, BMNH 1936.11.2.588–591, 33–34°S 9–16°E, 1000m.

DISTRIBUTION. Only the type material is known.

#### DESCRIPTION

Based on type material. Females 4–5mm.

Rostrum very small.

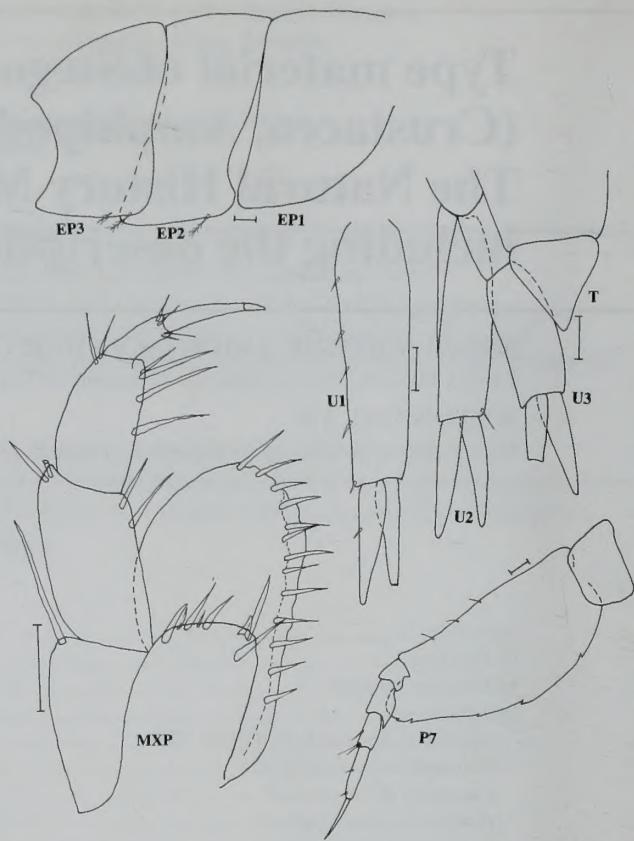


Fig. 1 *Andaniexis australis*, female cotype.

Antennae short. Antenna 1 longer than antenna 2; flagellum 6-articulate; accessory flagellum article 2 absent. Antenna 2 peduncle (articles 3–5) shorter than flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

Epistome produced laterally; rectangular with a long ridge on each side.

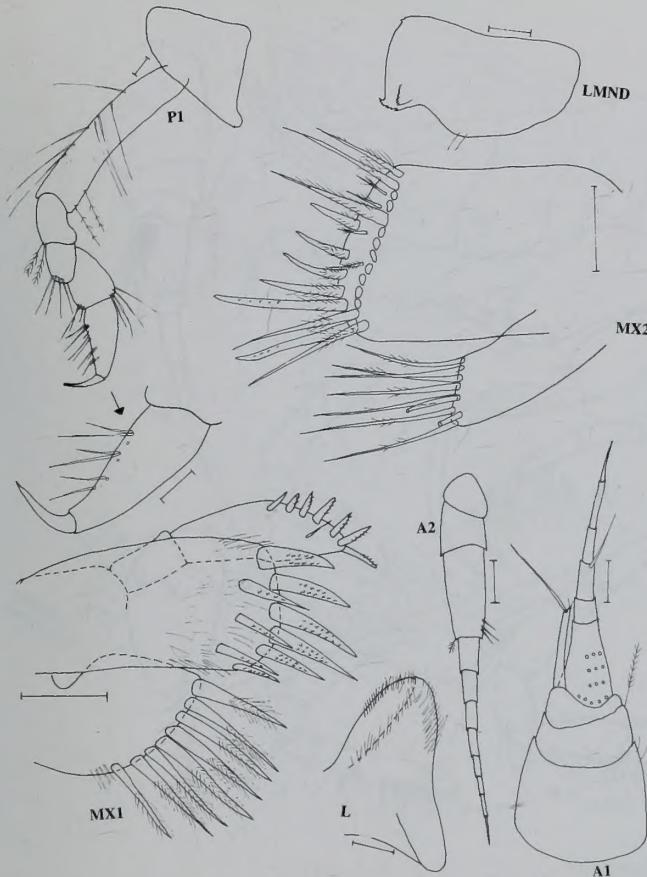
Epistomal plate (medial keel) produced; small elongate medial ridge exceeding along the entire epistome.

Mandible incisor transverse; incisor smooth; left lacinia mobilis present, reduced, distally straight, not conical.

Maxilla 1 palp 2-articulate, oval, apex reaching beyond outer plate; outer plate distally rounded, ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 ordinary (similar to ST 2–4), gap between ST5 and ST7 present, ST A–C present and part of second row; inner plate with a weakly developed shoulder; setae pappose.

Maxilla 2 ordinary; outer plate setae without distal hooks or cleft; inner plate setae row A covering the entire margin, clearly separated from row B, row A setae pappose; 3–4 first setae pectinate distally; row B setae proximally pappose, distally with cusps present; row C present; row D present, 1–3 long setae distally, setae slender.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate with 1 nodular seta; medial setae-row present, not reduced, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row present, but reduced to one or two setae, conspicuously large and strong; outer plate outer setae-row present, setae submarginal, attached normally, long robust, straight; inner setae-row present, well developed, setae long robust, slender, appressed to outer setae-row; distal setae-group absent.



**Fig. 2** *Andaniexis australis*, female cotype.

Labrum very short; lobes symmetrical and reduced.

Labium distally broad, oval.

Coxal plates and basis of pereopods smooth; coxae 1–3 contiguous.

Pereopod 1 coxa not as deep as basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length:breadth exceeding 1.5, posterior margin with long plumose setae distally; propodus subovate, palm absent.

Pereopod 4 coxa posteroventral lobe small, reaching about the base of the 6th pereon segment; basis anterior and posterior margins without long setae, with plumose setae on distal anterior margin, no plumose setae on distal posterior margin; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion conspicuous, rounded posteriorly, without a row of long plumose setae.

Pereopod 7 basis anterior margin concave, distally rounded, no medial row of setae.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present.

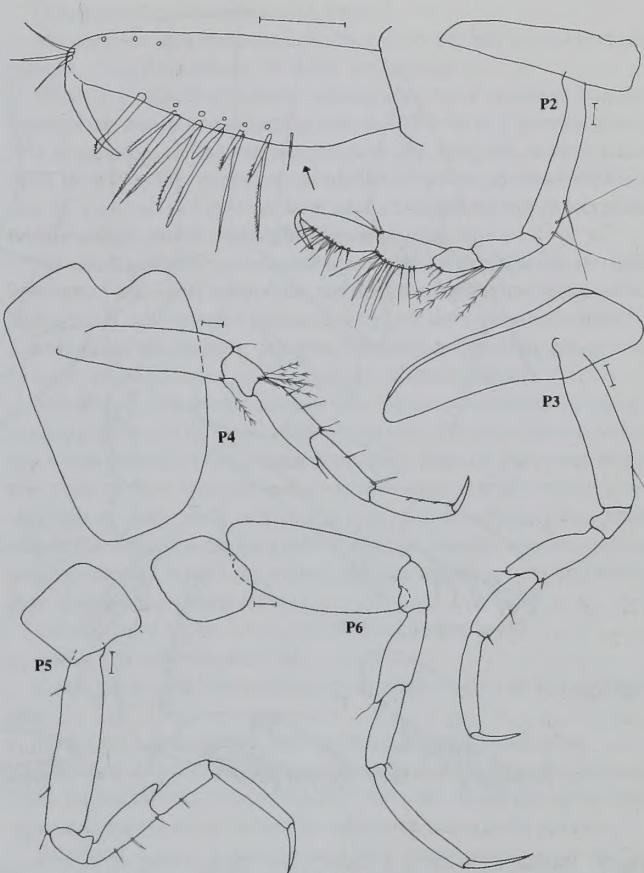
Uropod 1 peduncle longer than rami, outer ramus longer than inner.

Uropod 2 peduncle longer than rami, outer ramus slightly longer than inner. Uropod 3 peduncle longer than rami, outer ramus 2-articulate, outer ramus equal to inner.

Telson as long as broad, shorter than peduncle uropod 3, entire, apically pointed.

MALE. Unknown.

REMARKS. This species was originally described by K.H. Barnard



**Fig. 3** *Andaniexis australis*, female cotype.

in 1932, and has later been redescribed by Barnard 1962, 1964) and Ledoyer (1986). However, neither of these redescriptions were made based upon the type material. Consequently, both *Andaniexis americana* sp.nov. (see below) and *Andaniexis gloriosa* sp. nov. (see below) were wrongly identified as *A. australis* s.s.

The combination of a rectangular coxa 4, a concave anterior margin of pereopod 7 and the presence of only one nodular seta on the inner plate of the maxilliped is unique for this species within the genus (note: the last character is unknown for *A. oculatus*). From the description of *A. oculatus*, it is not possible to separate *A. australis* from *A. oculatus*. However, until material of the latter has been made available for examination, the two species are not put into synonymy.

#### *Andaniexis americana* sp.nov.

(Figs 4–5)

*Andaniexis australis* Barnard 1964: 13 fig. 9 (non *A. australis* K.H. Barnard, 1932)

MATERIAL EXAMINED. Holotype, Station V-15-69 (see Barnard 1964), females 3mm, 10°13'S 80°05'W, Dec. 9, 1958, 6324–6328m. Paratype, female 2.6mm (see Barnard 1964).

DISTRIBUTION. Only type material is known.

#### DESCRIPTION

Rostrum very small.

Antennae short. Antenna 1 longer than antenna 2; flagellum 5-articulate; accessory flagellum article 2 present. Antenna 2 peduncle

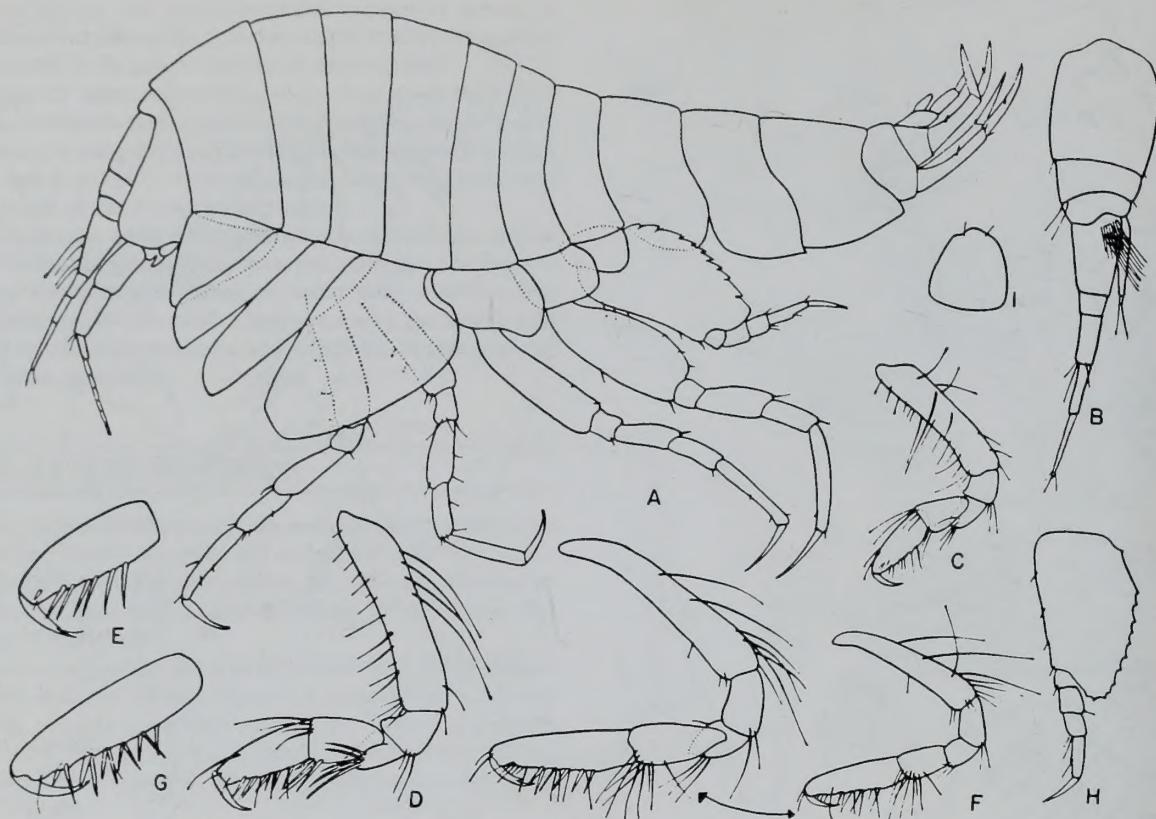


Fig. 4 *Andaniexis americana* sp.nov., from: Barnard 1964:14, fig.9 '*Andaniexis australis*'.

(articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 longer than article 5.

Epistome produced laterally, rectangular with a long ridge on each side; epistomal plate (medial keel) produced into a small elongate medial ridge exceeding along the entire epistome.

Mouthparts not elongate or pointed.

Mandible incisor transverse; smooth; left lacinia mobilis present, reduced, laterally straight, not conical.

Maxilla 1 palp 2-articulate, oval, apex reaching beyond outer plate; outer plate distally rounded; ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 ordinary (similar to ST 2–4), gap between ST 5 and ST 7 present, ST A–C present and part of second row; inner plate with a weakly developed shoulder, setae pappose.

Maxilla 2 ordinary; outer plate setae without distal hooks or cleft; inner plate setae row A covering the entire margin, clearly separated from row B, row A setae pappose, 3–4 first setae pectinate distally; row B setae proximally pappose, distally with cusps absent; row C present; row D present, 1–3 long setae distally, slender.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate with 1 nodular setae; medial setae-row present, not reduced, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row absent; outer plate outer setae-row present, submarginal, setae attached normally, setae long robust; inner setae-row present, well developed, setae long robust, slender, appressed to outer setae-row; distal setae-group absent.

Labrum very short; lobes symmetrical and reduced.

Labium unknown.

Coxal plates and basis of pereopods smooth; coxae 1–3 contiguous.

Pereopod 1 coxa not as deep as basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length:breadth

exceeding 1.5; ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe small, reaching about the base of the 6th pereon segment; basis anterior and posterior margins without long setae, with plumose setae on distal anterior margin, no plumose setae on distal posterior margin; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion conspicuous, rounded posteriorly, without a row of long plumose setae.

Pereopod 7 basis anterior margin concave; distally rounded; no medial row of setae.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present.

Uropod 1 peduncle longer than rami, outer ramus longer than inner.

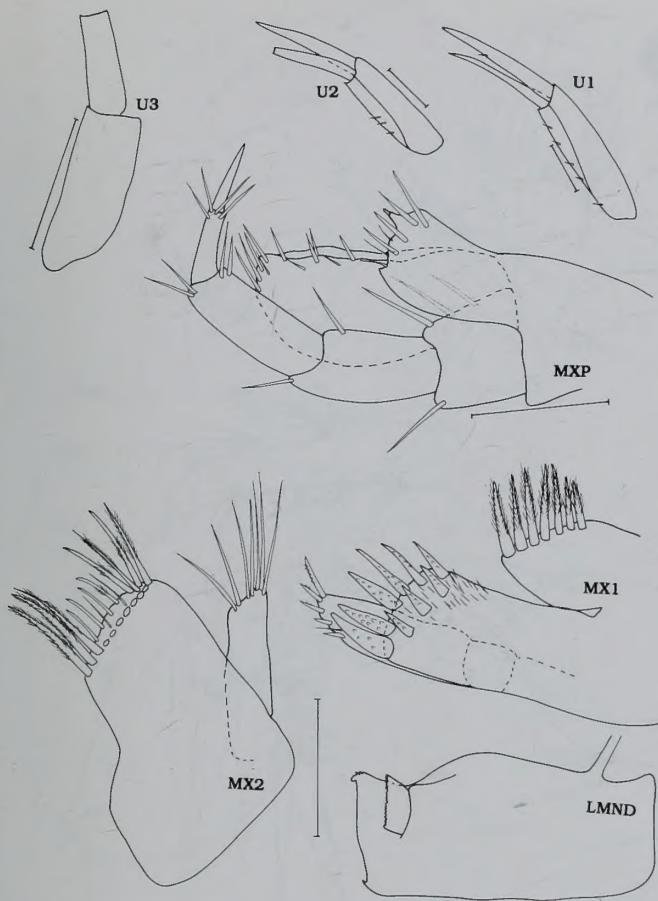
Uropod 2 peduncle longer than rami, outer ramus as long as inner.

Uropod 3 peduncle longer than rami, outer ramus 2-articulate.

Telson as long as broad, shorter than peduncle uropod 3, entire; apically rounded, submarginal setae apically.

MALE. Unknown.

REMARKS. This is the only recorded species of *Andaniexis* from the west coast of the American continent. The present species is a typical member of this genus, but is separated from all other known species of this genus by its very broad and powerful lacinia mobilis (left mandible only). As in *A. australis*, *A. gracilis* Berge & Vader, 1997a, *A. oculatus* Birstein & Vinogradov, 1970 and *A. stylifer*



**Fig. 5** *Andaniexis americana* sp.nov., holotype.

Birstein & Vinogradov, 1960, the anterior margin of pereopod 7 is slightly concave, while only two other known species, *A. australis* and *A. gloriosa* (see below), share its state of having just one nodular seta on inner plate of the maxilliped. Furthermore, the present species has coxa 4 'heart'-shaped, a character otherwise only found in *A. gracilis*, *A. mimonectes* Ruffo, 1975 and *A. tridentata* Ledoyer, 1986.

#### *Andaniexis gloriosa* sp. nov.

(Figs 6–7)

*Andaniexis australis* Ledoyer 1986: 953–954, fig. 375. (non *A. australis* K.H. Barnard, 1932)

MATERIAL EXAMINED. Holotype, female 7mm, st. CH90 (see Ledoyer 1986). Paratypes 4 females, 7–10 mm, st. CH 87 (see Ledoyer 1986), 3716m. Additional material, immature 2,5 mm, st. DE 12 (see Ledoyer 1986), 2500m.

DISTRIBUTION. Only known from the type locality (Madagascar).

#### DESCRIPTION

Rostrum very small.

Antennae short. Antenna 1 shorter than antenna 2; flagellum 5-articulate; accessory flagellum article 2 present. Antenna 2 peduncle (articles 3–5) as long as flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

Epistome produced laterally, rectangular with a long ridge on each side; epistomal plate (medial keel) produced into a small elongate medial ridge exceeding along the entire epistome.

Mouthparts not elongate or pointed.

Mandible incisor transverse; incisor smooth; left lacinia mobilis present, reduced, laterally straight, not conical.

Maxilla 1 palp 2-articulate, rectangular, apex reaching beyond outer plate; outer plate distally rounded; ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 ordinary (similar to ST 2–4), gap between ST 5 and ST 7 present, ST A–C present, all part of second row; inner plate with a weakly developed shoulder, setae apposite.

Maxilla 2 ordinary, outer plate setae without distal hooks or cleft; inner plate setae row A covering the entire margin, clearly separated from row B, row A setae apposite, 3–4 first setae pectinate distally; row B setae proximally apposite, distally without cusps; row C present; row D present, 1–3 long setae distally, slender.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate with 1 nodular setae; medial setae-row absent; distal setae-row present, setae simple; inner setae-row present, row reduced to one or two setae, conspicuously large and strong; outer plate outer setae-row present, submarginal, setae attached normally, setae long robust, straight; inner setae-row present, well developed, setae long robust, slender, appressed to outer setae-row; distal setae-group absent.

Labrum very short; lobes symmetrical and reduced.

Labium distally broad, oval.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa not as deep as basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length:breadth exceeding 1.5; ischium distal posterior with margin plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe small, reaching about the base of the 6th pereon segment; basis anterior and posterior margins without long setae, without plumose setae on distal anterior and posterior margins; ischium without plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion conspicuous, rounded posteriorly; without a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus longer than inner. Uropod 2 peduncle longer than rami, outer ramus longer than inner. Uropod 3 peduncle longer than rami, outer ramus 2-articulate, outer ramus longer than inner.

Telson longer than broad, shorter than peduncle uropod 3, entire, apically pointed, no submarginal setae on apically.

MALE. Unknown.

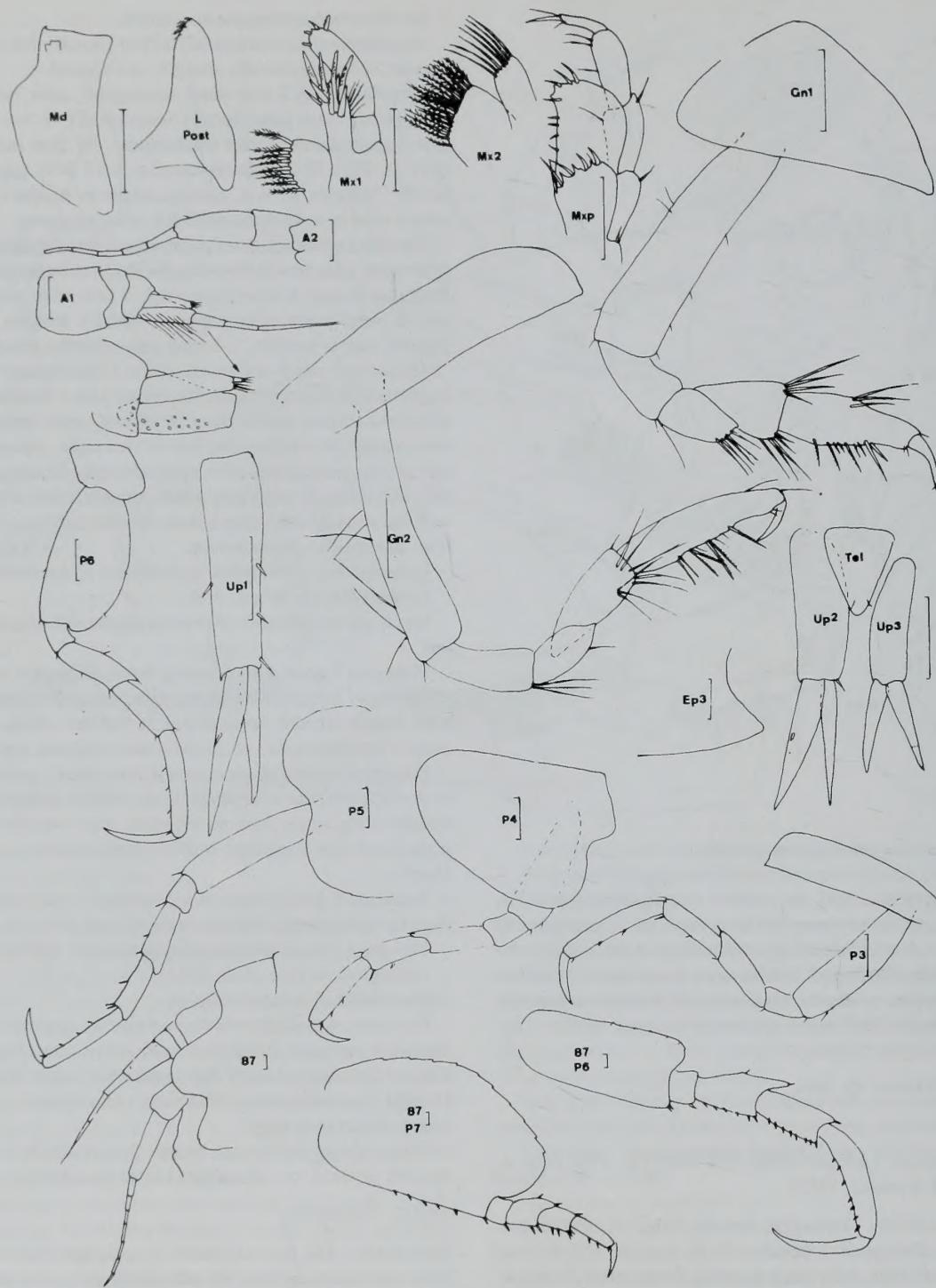
REMARKS. The present species is separated from all other members of *Andaniexis* by its relatively long and pointed telson. Furthermore, coxa 1 is relatively long and pointed (triangular), and is thus more similar to that of *Andaniotes* Stebbing, 1897.

Unfortunately, the type material, borrowed from Museo Civico de Storia Naturale in Verona, Italy, disappeared in the mail. Thus, at present, there exists, to the authors' knowledge, no registered material of this species.

#### *Andaniexis pelagica* sp.nov.

(Figs 8–10)

*Andaniexis australis* Barnard 1962: 38–40, figs. 24, 25 (immature 9 & 5.5 mm only, not immature 4.0, 2.0 & 1.5).



**Fig. 6** *Andaniexis gloriosa* sp.nov., from: Ledoyer 1986:955, fig.375 '*Andaniexis australis*'.

**MATERIAL EXAMINED.** Holotype, *Vema* Station 53 (see Barnard 1962), immature female 9.0 mm, Cape Basin, 4893 m. Paratype, *Vema* Station 53, immature 5.5 mm.

**DISTRIBUTION.** Known from type locality only.

**DESCRIPTION.** Biology: pelagic (Barnard 1962).

Rostrum very small.

Antennae elongate. Antenna 1 shorter than antenna 2; flagellum 3-articulate; accessory flagellum article 2 absent. Antenna 2 peduncle

(articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

Epistome produced laterally, rectangular with a long ridge on each side; epistomal plate (medial keel) produced into a small elongate medial ridge exceeding along the entire epistome.

Mouthparts not elongate or pointed.

Mandible incisor transverse; incisor smooth; left lacinia mobilis present, reduced, laterally straight, not conical.

Maxilla 1 palp 2-articulate, oval, apex reaching beyond outer

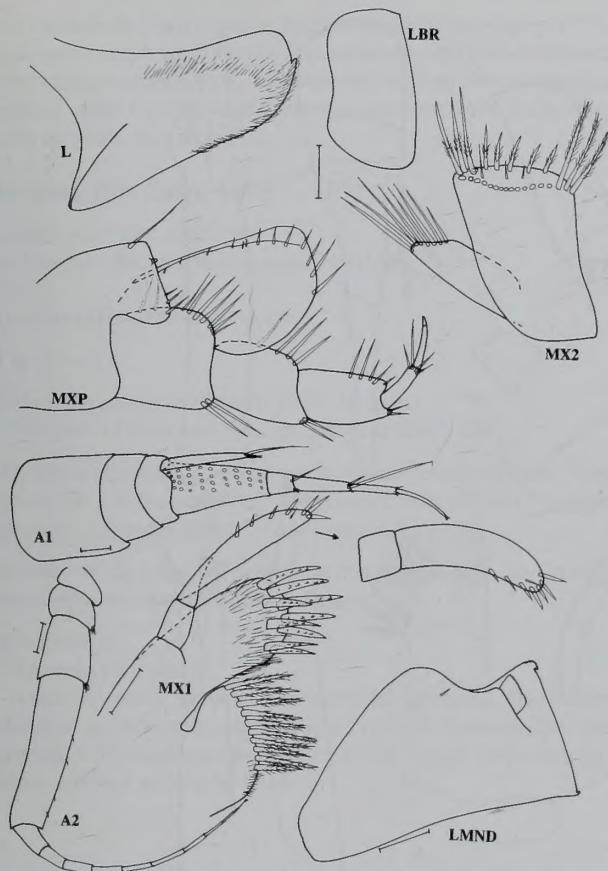


Fig. 7 *Andaniexis gloriosa* sp.nov., holotype.

plate; outer plate distally rounded; ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 ordinary (similar to ST 2–4), gap between ST 5 and ST 7 present, ST A–C present and part of second row; inner plate with a weakly developed shoulder, setae pappose.

Maxilla 2 ordinary, outer plate setae without distal hooks or cleft; inner plate setae row A covering the entire margin, appressed to row B, row A setae pappose, 3–4 first setae pectinate distally; row B setae proximally pappose, distally with cusps present; row C present; row D present, reduced, 1–3 long setae distally, slender.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple

(pointed); inner plate with 2 nodular setae; medial setae-row present, not reduced, transverse, simple; distal setae-row present, setae simple; inner setae-row present, row reduced to one or two setae, conspicuously large and strong; outer plate outer setae-row present, marginal, setae attached normally, setae long robust, straight; inner setae-row present but strongly reduced, setae short simple, slender, appressed to outer setae-row; distal setae-group absent.

Labrum very short; lobes symmetrical and reduced.

Labium distally broad, oval.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa not as deep as basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1, ischium elongate, ratio length:breadth exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe small, reaching about the base of the 6th pereon segment; basis anterior and posterior margins without long setae, plumose setae on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion rudimentary, no row of long plumose setae.

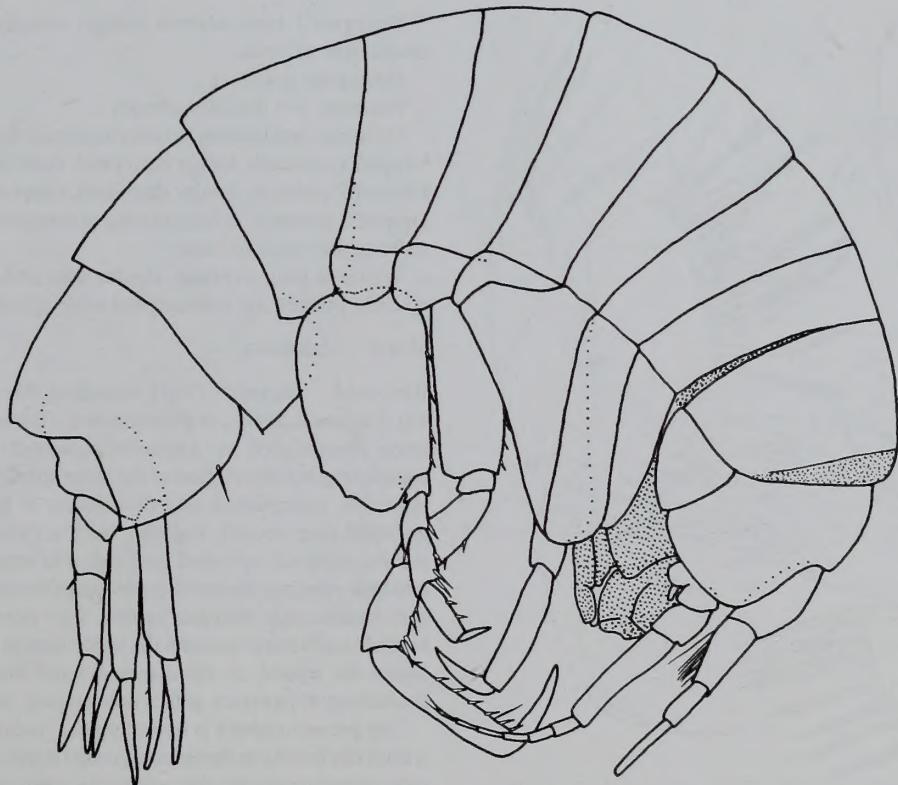


Fig. 8 *Andaniexis pelagica* sp.nov., from: Barnard 1962:38, fig. 24 '*Andaniexis australis*'.

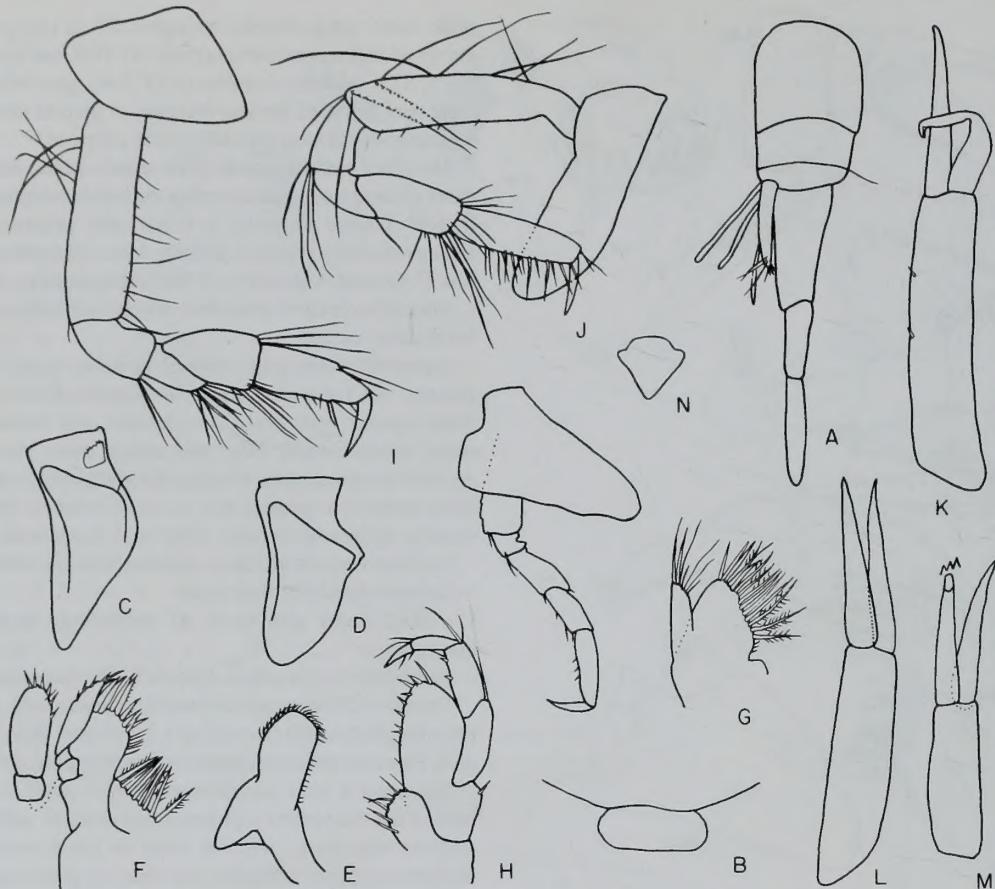


Fig. 9 *Andaniexis pelagica* sp.nov., from: Barnard 1962:38, fig. 25 '*Andaniexis australis*'.

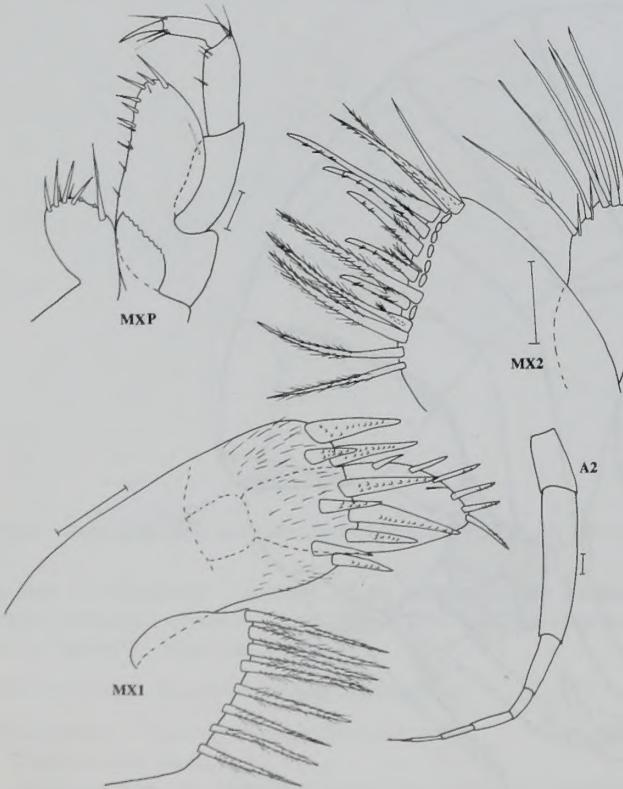


Fig. 10 *Andaniexis pelagica* sp.nov., holotype.

Pereopod 7 basis anterior margin straight, distally rounded, no medial row of setae.

Oostegites unknown.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus as long as inner. Uropod 2 peduncle longer than rami, outer ramus as long as inner. Uropod 3 peduncle at least as long as rami, outer ramus 2-articulate, outer ramus equal to inner.

Telson as long as broad, shorter than peduncle uropod 3, entire, apically pointed, no submarginal setae apically.

#### MALE. Unknown.

**REMARKS.** Barnard (1962) identified five specimens ('9.0, 5.5, 4.0, 2.0, and 1.5 mm., sexes unknown' (Barnard 1962: 40) from the same *Vema* station as '*Andaniexis australis* (?)', due to the inadequate original description of the latter species (K.H.Barnard 1932). However, examination and description of the type material of *A. australis* (see above), together with a closer examination of the present material, revealed that it should actually be separated into two new species: *Andaniexis pelagica* (immature 9.0 and 5.5 mm) and *Andaniopsis africana* sp.nov. (see below). [In fact, Barnard himself must have reached the same conclusion after he had published his results, as there was a small note in one of the vials containing *A. pelagica* with a note stating 'holotype'.]

The present species is not a 'typical' member of *Andaniexis*, i.e. it does not belong to the *abyssi*-group (Berge & Vader 1997a), but is more closely related to the '*tridentata*-group' (*A. tridentata* Ledoyer, 1986 and *A. spinescens* Alcock, 1894, see Berge & Vader 1997a),

and the more distinctive genus *Parandaniexis* Schellenberg, 1929. It is, however, separated from all *Parandaniexis* spp by the absence of a subchelate pereopod 4. Furthermore, of the above mentioned species, only *Parandaniexis inermis* Ledoyer, 1986 lacks dorsal teeth on pleon segments 1–3.

### *Andaniopsis* Sars, 1895

*Andaniopsis* Sars, 1895: 208.

*Andaniopsis* Barnard & Karaman 1991: 678.

#### *Andaniopsis africana* sp.nov.

(Figs 11–12)

*Andaniexis australis* Barnard 1962: 38 (part)

? 'Unknown Genus and Species' Barnard 1967: 150

MATERIAL EXAMINED. Holotype, immature female 4.0 mm, 'Vema' station 53 (see Barnard 1962: 40): Cape Basin, 4893 m. Paratypes, immature 2.0 and 1.5 mm, 'Vema' station 53.

DISTRIBUTION. Known only from the type locality (and possibly from the west coast of Mexico). Pelagic.

#### DESCRIPTION

Rostrum very small.

Antennae short. Antenna 1 longer than antenna 2; flagellum 4-articulate; accessory flagellum article 2 present. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 as long as article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) produced into a large conspicuous keel.

Mouthparts not elongate or pointed.

Mandible incisor transverse; toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rounded; ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 ordinary (similar to ST 2–4), gap between ST 5 and ST 7 present, ST A–C present and part of second row; inner plate without a well developed shoulder, setae pappose.

Maxilla 2 ordinary, outer plate setae without distal hooks or cleft; inner plate setae row A covering the entire margin, appressed to row B, row A setae pappose, 3–4 first setae weakly pappose proximally, slender distally; row B setae proximally simple, distally with cusps absent; row C absent; row D absent.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate not exceeding base of palp article 2; with 2 nodular setae; medial setae-row present, not reduced, transverse, setae pectinate; distal setae-row absent; inner setae-row present, row reduced to one or two setae, setae conspicuously large and strong; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short, straight; inner setae-row present but strongly reduced, setae short simple, slender, parallel but not appressed to outer setae-row; distal setae-group absent.

Labrum not reduced; lobes asymmetrical and reduced.

Labium distally broad, oval.

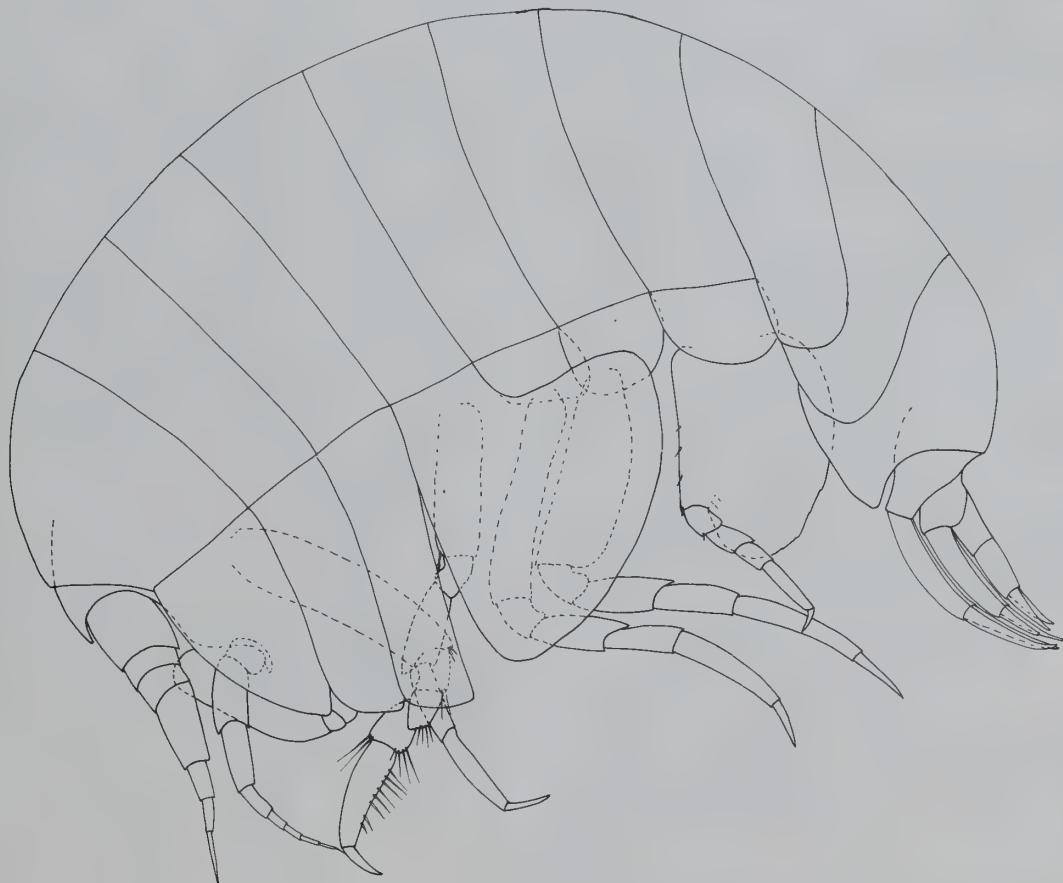


Fig. 11 *Andaniopsis africana* sp.nov., holotype (see scale 3 on fig. 12).

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subrectangular.

Pereopod 2 general appearance like pereopod 1, ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe medium sized, not reaching the base of the 7th pereon segment; basis anterior and posterior margins without long setae, plumose setae on distal anterior margin, no plumose setae on distal posterior margin; ischium without plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion conspicuous, rounded posteriorly, without a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, with a medial row of setae, setae short and robust.

Oostegites on pereopods 2–5; gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present.

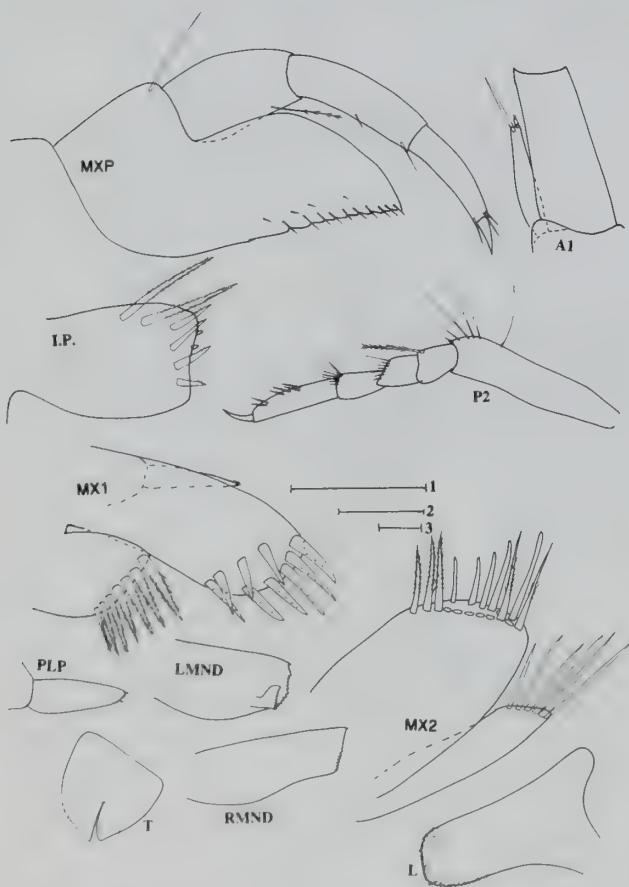
Uropod 1 peduncle longer than rami, outer ramus as long as inner.

Uropod 2 peduncle longer than rami, outer

ramus as long as inner. Uropod 3 peduncle at least as long as rami, outer ramus 1-articulate, outer ramus as long as inner.

Telson shorter than broad, shorter than peduncle uropod 3, cleft; apically rounded, submarginal setae on apex of each lobe.

MALE. Unknown



**Fig. 12** *Andaniopsis africana* sp.nov., holotype: PLP, MX 1 & MX2: scale 1, L, LMND, MND & T: scale 2; MXP & A1: scale 1 on fig. 14, P2: scale 3

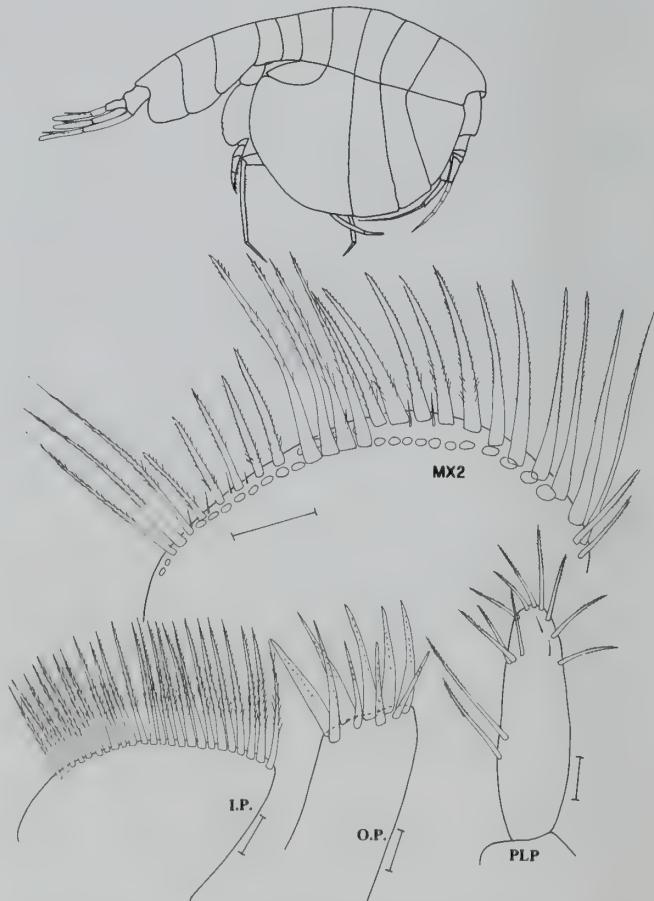
REMARKS. The present species is described herein in *Andaniopsis* as it resembles *Andaniopsis nordlandica* in some important characters: 1) transverse and toothed incisor and laterally expanded lacinia mobilis on the mandible, 2) reduced palp of the first maxilla, 3) general morphology of the maxilliped, 4) a large epistomal plate and 5) relatively long labrum with a well developed right lobe. However, the present species possesses a cleft telson, a character not found in *nordlandica* or in the closely related genus *Andaniella* Sars, 1895.

In 1967, Barnard described an immature specimen from a 'unknown genus and species' (Barnard 1967: 150). Although the epistome and labrum were damaged, and he did not describe the telson, the present species seems to be at least closely related to Barnard's specimen, if not even belonging to the same species. As some essential appendages were damaged, and since it has not been possible to examine the specimen, Barnard's specimen is referred to as an uncertain synonymy of the present new species. The only character that, at present, appears to separate Barnard's specimen as a distinct species from *africana*, is the unexpanded basis on pereopod 6 (expanded for *africana*).

ETYMOLOGY. The present species is the first species in the genus to be recorded from the southern hemisphere and more specifically from the coast of South Africa, hence its name *africana*.

### Bathystegocephalus Schellenberg, 1926

*Bathystegocephalus* Schellenberg, 1926: 221



**Fig. 13** *Bathystegocephalus globosus*, female (8mm) syntype.

***Bathystegocephalus globosus* (Walker, 1909)**

(Figs 13–15)

*Stegocephalus globosus* Walker 1909*Stegocephaloides valdiviae* Strauss ?1909*Bathystegocephalus globosus* Schellenberg, 1926*Bathystegocephalus globosus* Pirlot 1933*Bathystegocephalus globosus* Birstein & Vinogradov 1964

MATERIAL EXAMINED. Syntypes, BMNH 1909.1.29.17–31 (15 specimens: females and juveniles, 4.5–10mm)

DISTRIBUTION. Indian Ocean.

DESCRIPTION. Biology: pelagic.

Rostrum absent.

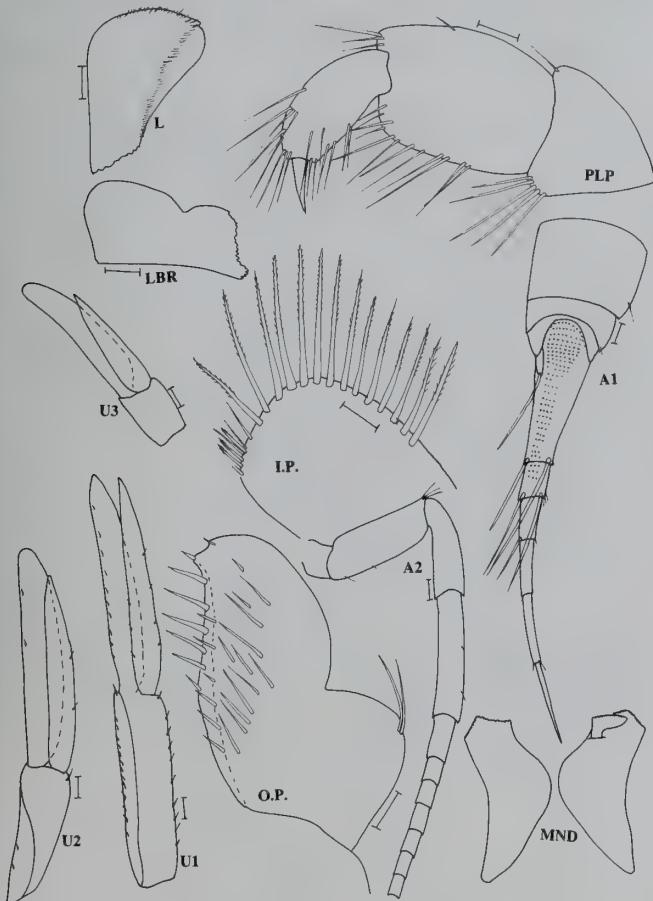
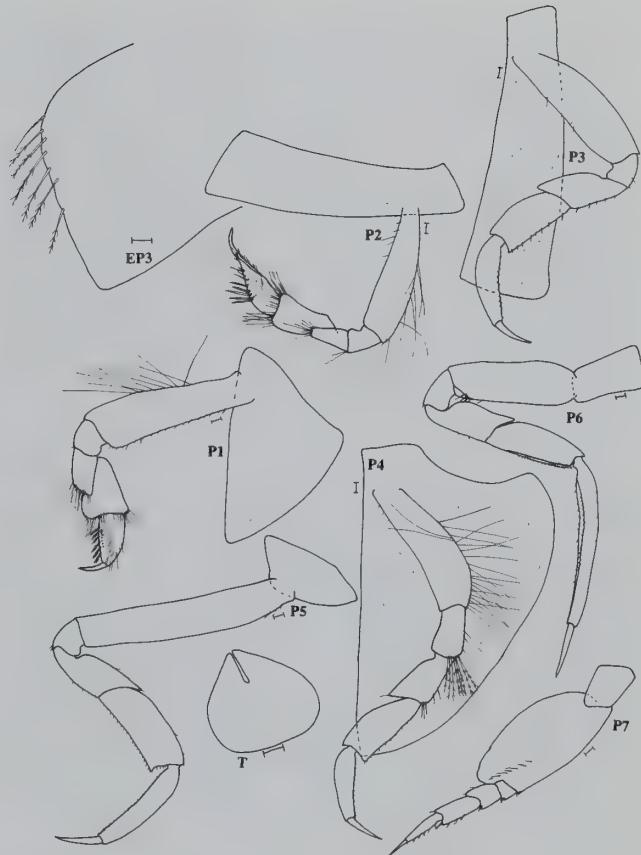
Antennae elongate. Antenna 1 shorter than antenna 2; flagellum 6-articulate; accessory flagellum article 2 absent. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 elongate, article 3 and 4 geniculate; article 4 shorter than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed.

Mandible incisor triangular; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, oval, apex reaching beyond outer plate; outer plate distally rectangular; ST in two parallel rows, first marginal and second submarginal, ST first row with 5 setae, ST 1 ordinary (similar to ST 2–4), ST 1–5 with one setae absent, ST 6

Fig. 14 *Bathystegocephalus globosus*, female (8mm) syntype.Fig. 15 *Bathystegocephalus globosus*, female (8mm) syntype.

absent, gap between ST 5 and ST 7 present, ST A–D present and part of second row; inner plate with a weakly developed shoulder, setae pappopectinate.

Maxilla 2 outer plate absent, inner plate setae row A covering the entire margin, appressed to row B, row A setae pappopectinate; row B setae proximally pappose, distally with cusps present; row C present; row D present, 1–3 long setae distally, with many small cusps distally.

Maxillipedal palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate without nodular setae; medial setae-row present, reduced, transverse, setae pectinate; distal setae-row present, reduced, setae simple; inner setae-row present, setae conspicuously large, cuspidate; outer plate outer setae-row present, marginal, setae attached normally, setae short and straight; inner setae-row present, well developed, setae long robust, slender, parallel to outer row but widely separated proximally; distal setae-group present, setae attached normally, long robust.

Labrum very short; lobes symmetrical and reduced.

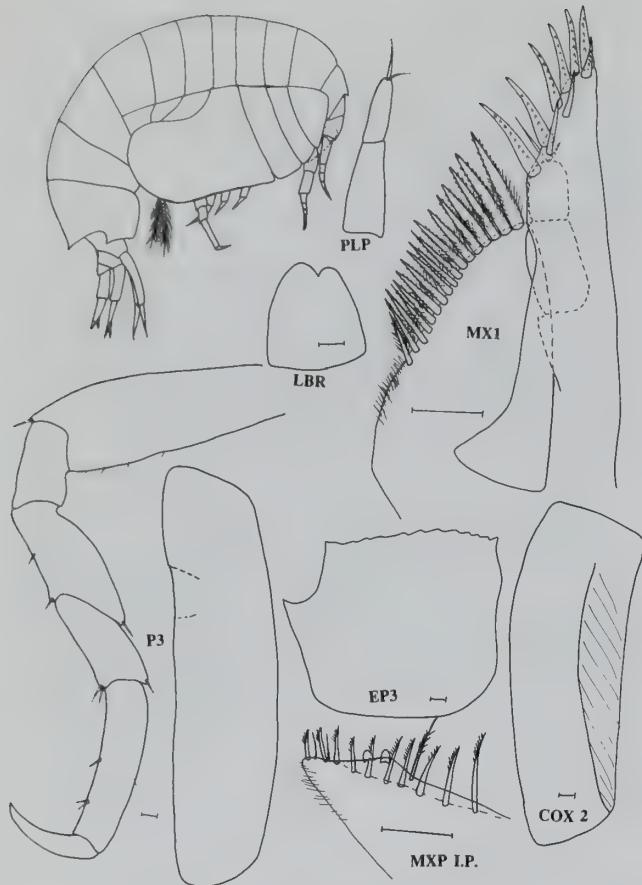
Labium distally broad, oval.

Coxal plates and basis of pereopods covered with very short setules. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subovate.

Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subovate palm absent.

Pereopod 4 coxa posteroventral lobe medium sized, not reaching the base of the 7th pereon segment; basis anterior margin without long setae, posterior margin with long setae, without plumose setae



**Fig. 16** *Phipsia gibbosa*, immature female, Bioice st.570.

on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin.

Pereopod 6 elongate, basis posteriorly expanded, expansion rudimentary, without a row of long plumose setae; carpus and propodus anteriorly concave.

Pereopod 7 basis anterior margin straight, distally rounded, with a medial row of long setae.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 absent. Uropod 1 peduncle shorter than rami, outer ramus longer than inner. Uropod 2 peduncle shorter than rami, outer ramus longer than inner. Uropod 3 peduncle shorter than half the length of rami, outer ramus 1-articulate, outer ramus longer than inner.

Telson as long as broad, as long as peduncle uropod 3, cleft, apically rounded, no submarginal setae on apex of each lobe.

**MALE.** Pereopod 2 and urosome ordinary (similar to females).

**REMARKS.** The present species is distinguishable from all other stegocephalid species by its elongate pereopod 6, reduced outer plate of maxilla 2 and the triangular shape of the mandibular incisor. In addition to this, its long and round coxae 1–4 give the anterior part of the body a conspicuously globular shape.

### *Phipsia* Stebbing, 1906

*Aspidopleurus* Sars, 1895: 203 (homonym, Pisces)  
*Phipsia* Stebbing, 1906: 89 (replacement name)

### *Phipsia gibbosa* (Sars, 1883)

(Figs 16–19)

*Stegocephalus gibbosa* Sars 1883

*Aspidopleurus gibbosa* Sars 1895

**MATERIAL EXAMINED.** Description based upon immature female, Bioice st. 570 (see Berge & Vader 1997d), checked with type (see Remarks).

**DISTRIBUTION.** North Atlantic.

**DESCRIPTION.** Biology: not pelagic, has been found on living *Lophelia* sp. (see Sars 1895 and W. Vader *pers. com.*).

Rostrum very small.

Antennae short. Antenna 1 longer than antenna 2; flagellum 6-articulate; accessory flagellum article 2 absent. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

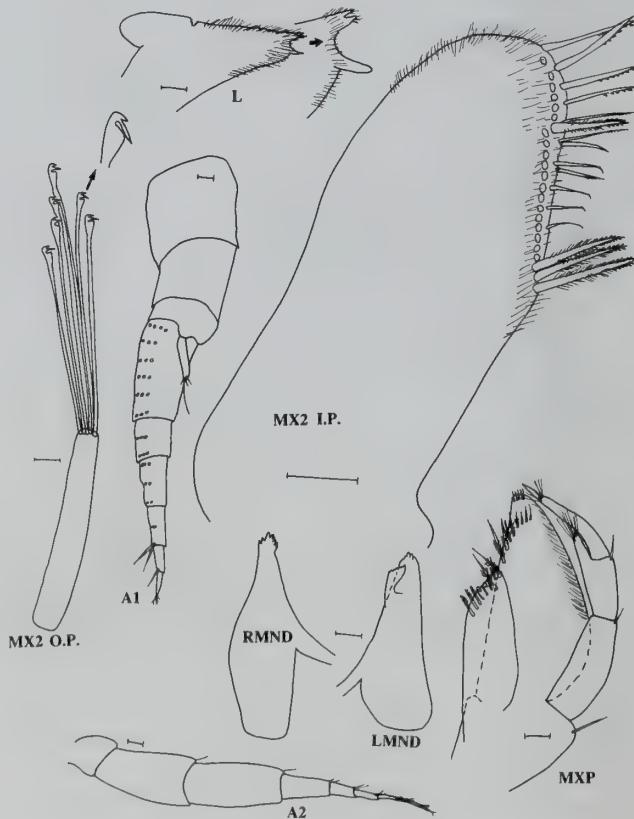
Epistome curved (convex) and smooth; epistomal plate (medial keel) produced into a large conspicuous medial keel.

Mouthparts not elongate or pointed.

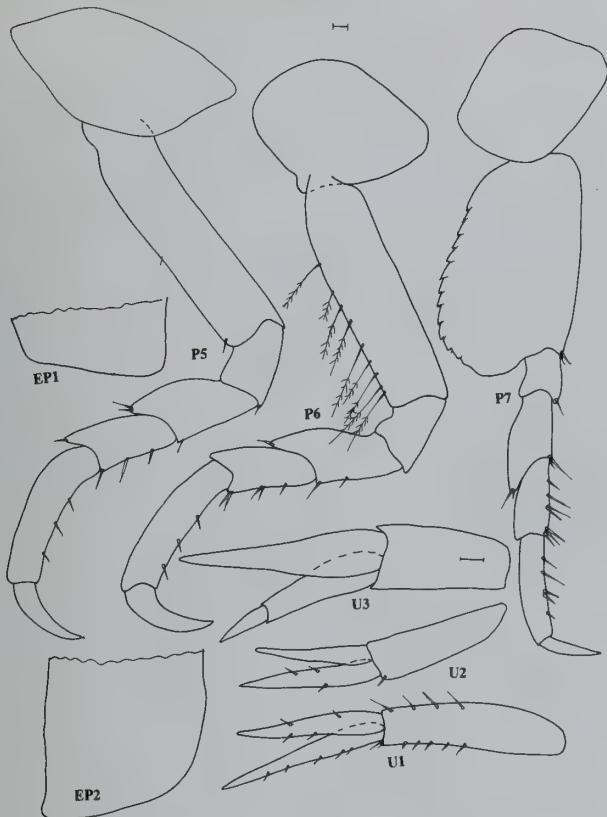
Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 2-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in a pseudocrown (see below), ST first row with 6 setae (ST1–5, ST7), ST 1 conspicuously enlarged, gap between ST 5 and ST 7 absent; ST A and B present, located distally, part of first row, ST C present, ST D absent; inner plate with a well developed shoulder, setae pappopectinate.

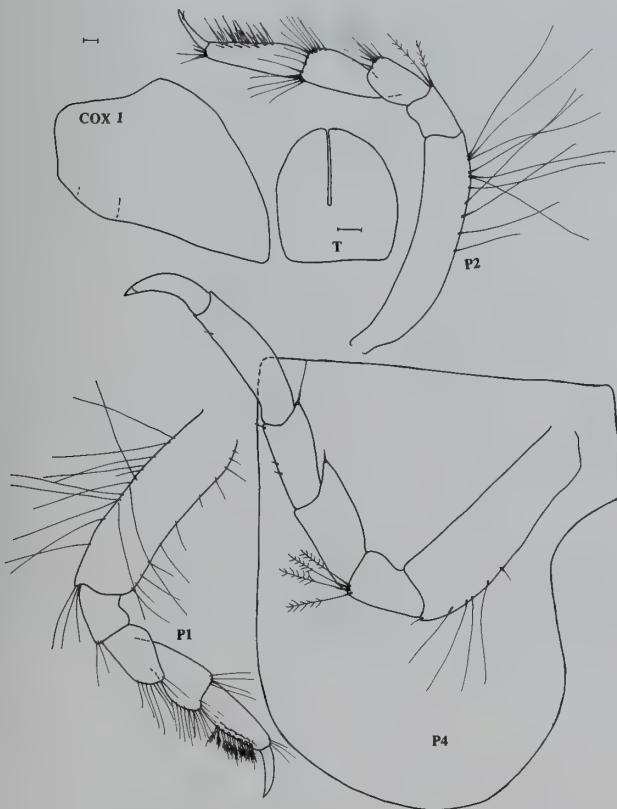
Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft present; inner plate setae row A covering



**Fig. 17** *Phipsia gibbosa*, immature female, Bioice st.570.



**Fig. 18** *Phippsia gibbosa*, immature female, Bioice st.570.



**Fig. 19** *Phippsia gibbosa*, immature female, Bioice st.570.

about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally simple, distally with cusps present; row C present; row D present, expanded, row elongated towards and beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distal inner margin greatly produced, dactylus distally simple (pointed); inner plate with 2 nodular setae; medial setae-row present, not reduced, vertical, setae pectinate; distal setae-row present, setae simple; inner setae-row present, row reduced to one or two setae, setae conspicuously large and strong; outer plate outer setae-row present, marginal, setae attached normally, setae short, strongly curved upwards (hooks); inner setae-row present, well developed, setae long robust, setae pappose, proximally parallel to outer, distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical; right lobe not reduced, left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subrectangular.

Pereopod 2 longer and thinner than pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe very large, reaching beyond the base of the 7th pereon segment; basis anterior margin without long setae, posterior margin with long setae, without plumose setae on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly unexpanded, with a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, no medial row of setae.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus longer than inner. Uropod 2 peduncle as long as rami, outer ramus shorter than inner. Uropod 3 peduncle longer than half the length of rami, outer ramus 2-articulate, outer ramus shorter than inner.

Telson longer than broad, longer than peduncle uropod 3, cleft; apically rounded, no submarginal setae on apex of each lobe.

**MALE.** Unknown.

**REMARKS.** Records at The Natural History Museum, London (see also Thurston & Allen, 1969) state that a type specimen of the present species is stored there, but that the validity of its status as a syntype is doubtful. The specimen in question was collected by G.O.Sars from the west coast of Norway, but the absence of a date leaves some doubt as to its type status.

The present species is easily distinguished from all other stegocephalid species due to its peculiar gibbous pleonite 3. For a revision of this genus, see Berge & Vader (2000).

### *Phippsiella* Schellenberg, 1925

*Phippsiella* Schellenberg 1925: 200

*Phippsiella rostrata* K.H. Barnard, 1932

(Figs 20–21)

*Phippsiella rostrata* K.H. Barnard 1932: 76

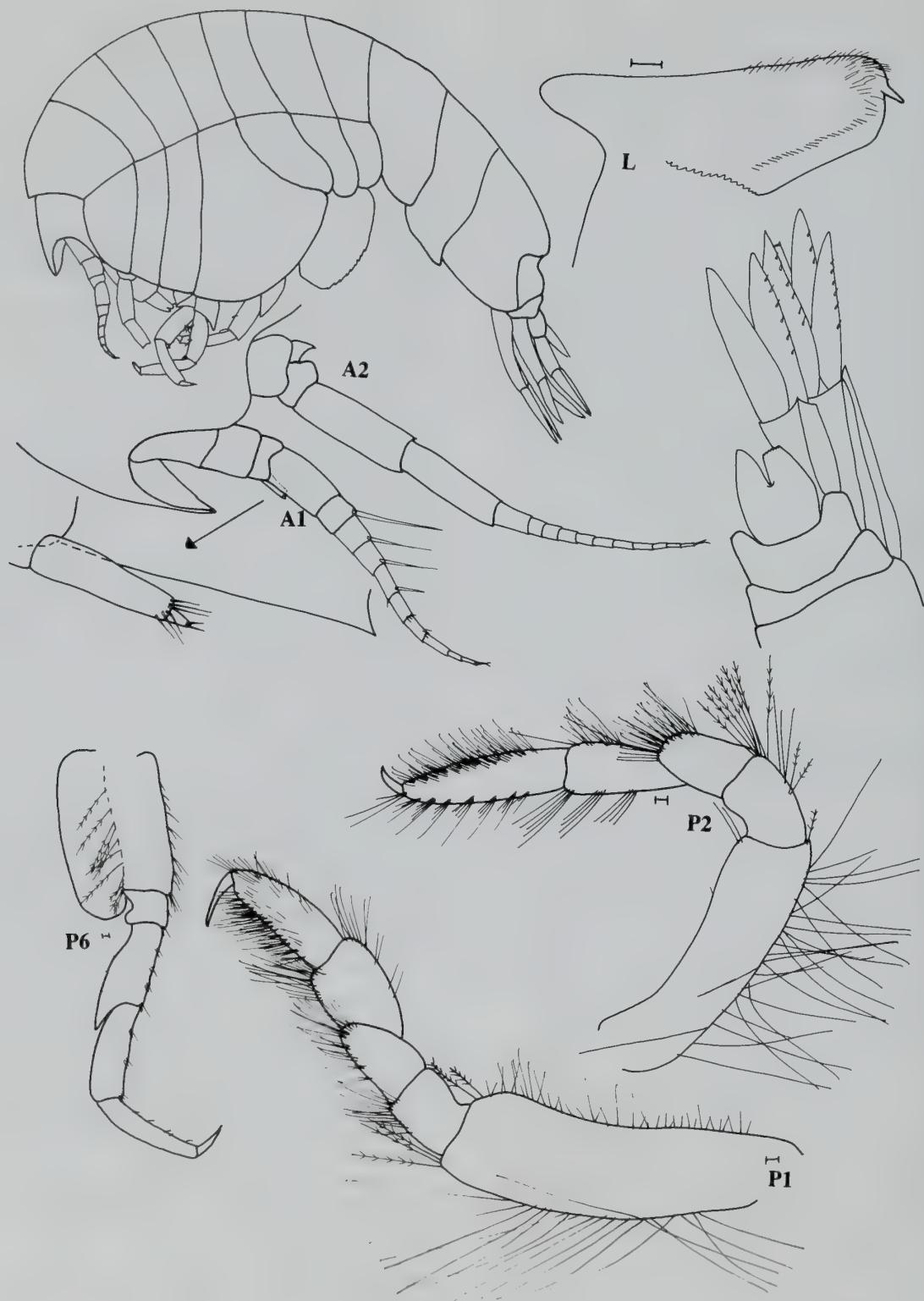


Fig. 20 *Phippiella rostrata*, Habitus: female (17mm) paratype, Urosome & L: male 17mm paratype.

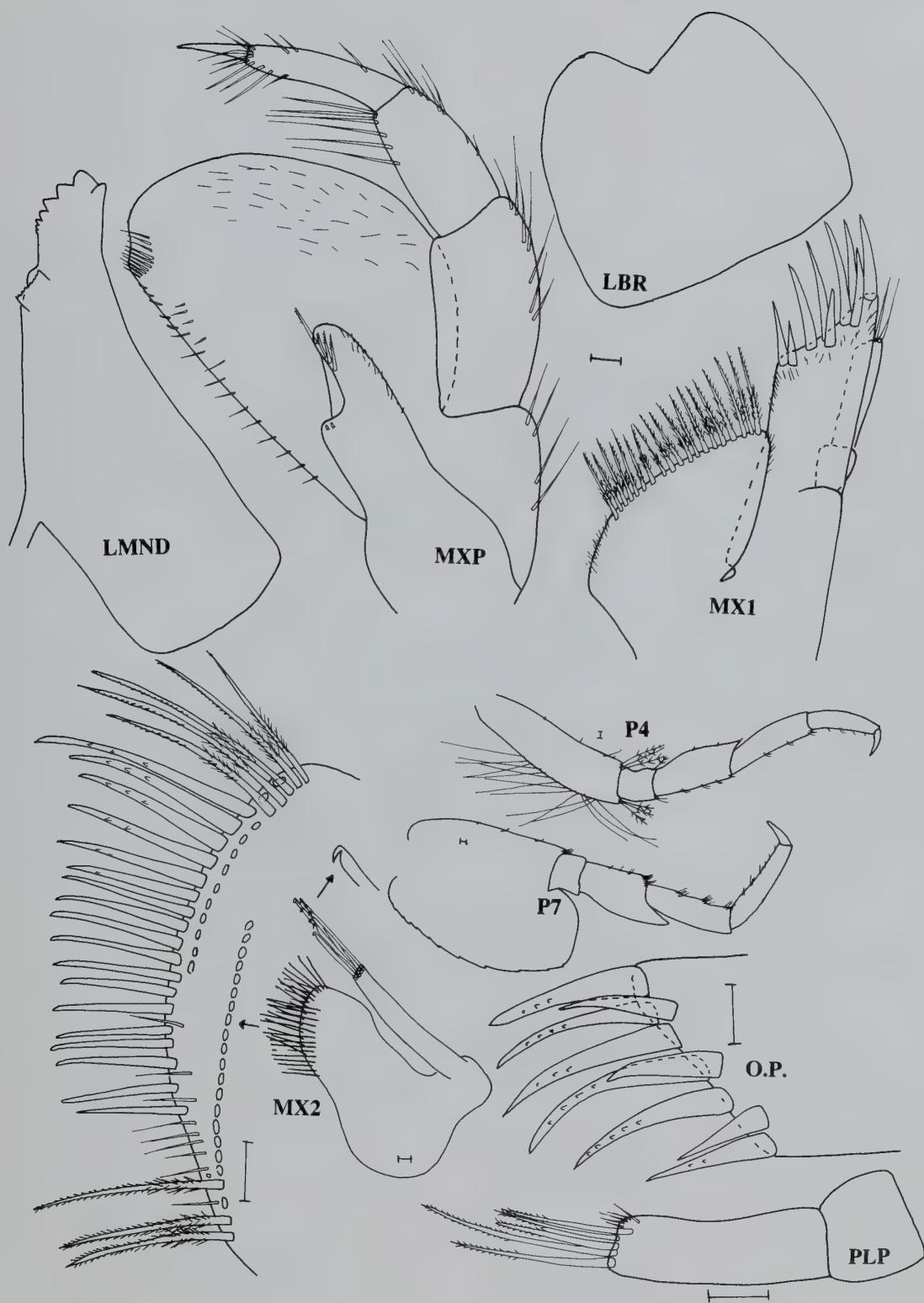


Fig. 21 *Phippsiella rostrata*, male (17mm) paratype.

MATERIAL EXAMINED. Syntypes, BMNH 1936.11.2.585–587; Discovery St 158 (see K.H. Barnard 1932), 1 male and 2 females (17–18 mm). Only the type material is known.

DISTRIBUTION. Known only from the type locality (South Georgia).

DESCRIPTION. Biology: not pelagic, otherwise unknown.

Rostrum powerful.

Antennae short. Antenna 1 shorter than antenna 2; flagellum 11-articulate; accessory flagellum article 2 present. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 longer than article 5.

Epistome curved (convex) and smooth. Epistomal plate (medial keel) not produced. Mouthparts not elongate or pointed.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 2-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in two parallel rows, first marginal and second submarginal, ST first row with 6 setae (ST1–5, ST7), ST 1 conspicuously enlarged, gap between ST 5 and ST 7 present; ST A–C present, part of first row, ST D absent; inner plate without a well developed shoulder, setae pappopectinate.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present; distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally simple, distally with cusps present; row C present; row D present, expanded, row elongated towards and beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate with 2 nodular setae; medial setae-row present, not reduced, transverse, setae pectinate; distal setae-row absent; inner setae-row absent; outer plate outer setae-row present, marginal, setae attached normally, setae short and strongly curved upwards (hooks); inner setae-row present, well developed, setae short simple and slender, proximally parallel to outer, distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical, left lobe weakly reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subrectangular.

Pereopod 2 general appearance like pereopod 1, ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe medium sized, not reaching the base of the 7<sup>th</sup> pereon segment; basis anterior margin without long setae, posterior margin with long setae, plumose setae on distal anterior and posterior margins; ischium without plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion conspicuous, rounded posteriorly, with a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, no medial row of setae.

Oostegites on pereopods 2–5.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus equal to inner. Uropod 2 peduncle longer than rami, outer ramus equal to inner. Uropod 3 peduncle longer than rami, outer ramus 1-articulate, outer ramus equal to inner.

Telson longer than broad, longer than peduncle uropod 3, cleft; apically open, no submarginal setae on apex of each lobe.

MALE. Pereopod 2 propodus equally sized in males and females. Urosome ordinary (similar to females).

REMARKS. This species is easily distinguished from all congeners by its long rostrum, but it has some affinities with *Stegocephalus inflatus* Krøyer, 1842. However, the morphology of both the mouthparts and of the basis of pereopod 7 strongly suggests that this species should be retained in the genus *Phippsiella*.

### *Stegocephalooides* Sars, 1895

*Stegocephalooides* Sars 1895: 201

#### *Stegocephalooides attingens* K.H. Barnard, 1932

(Figs 22–25)

*Stegocephalooides attingens* K.H. Barnard 1932: 131 (3 of 4 specimens only)

? *Stegocephalooides attingens* Barnard 1961: 60

? *Stegocephalooides attingens* Griffiths 1975: 167

MATERIAL EXAMINED. Syntypes, BMNH 1928.4.13.41–44; 3 specimens (but see below): female, male and immature, 5–8 mm, Cape Point, South Africa, 500–1000m. Additional material: SAM A4423, 4 specimens, Cape Point.

DISTRIBUTION. South Africa to (?) Angola, 990–1400m.

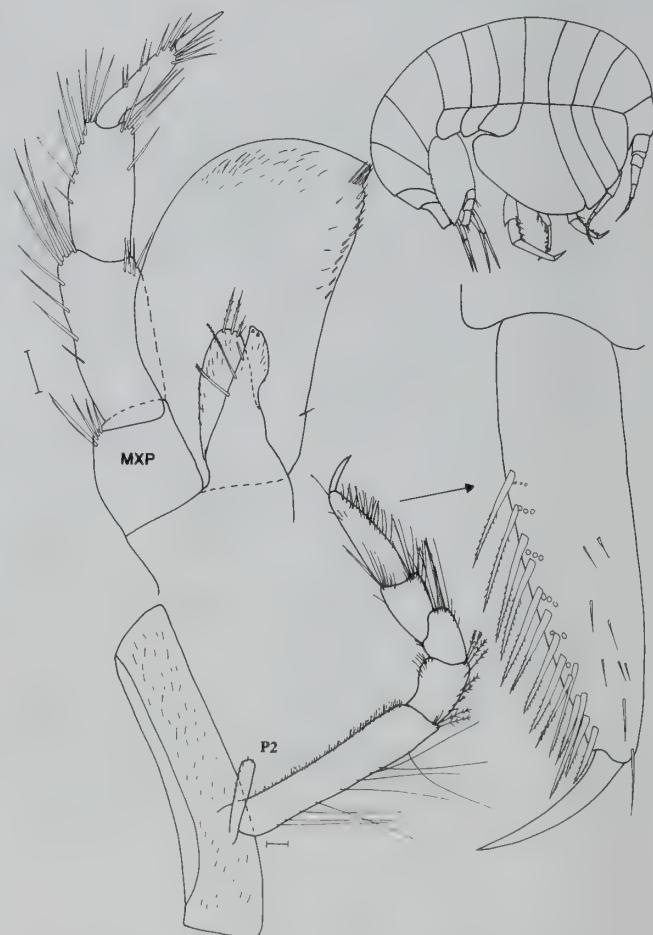
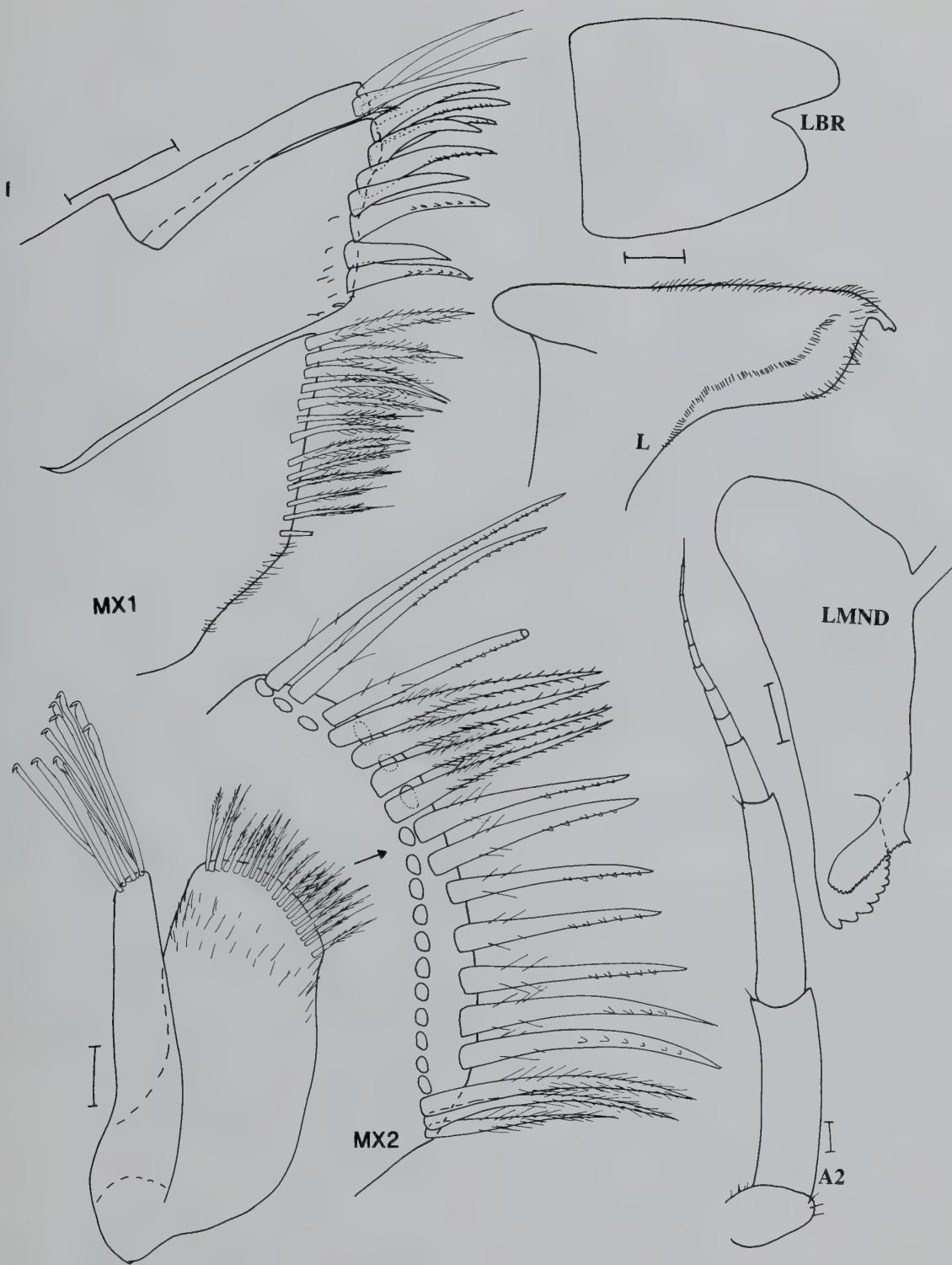


Fig. 22 *Stegocephalooides attingens*, female (8mm) cotype.



**Fig. 23** *Stegocephalides attingens*, female (8mm) cotype.

**DESCRIPTION.** Biology: not pelagic, otherwise unknown. Based on cotype, female 8 mm.

Rostrum very small.

Antennae short. Antenna 1 equal to antenna 2; flagellum 4-articulate; accessory flagellum article 2 absent. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 about as long as 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced. Mouthparts not elongate or pointed.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate and apex reaching beyond outer plate; outer plate distally rectangular; ST in a pseudocrown, ST first row with 6 setae (ST1–5,

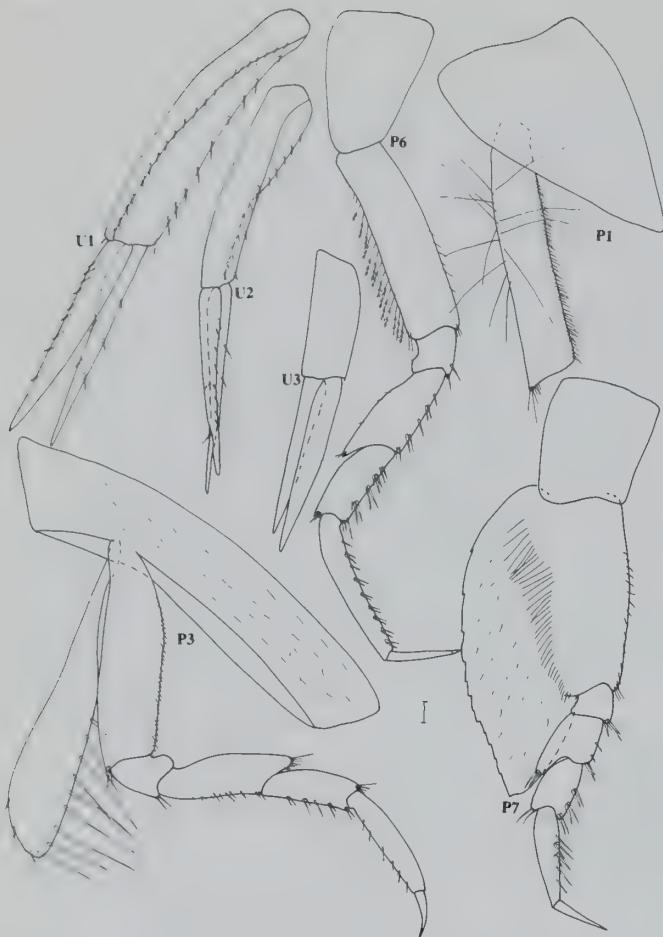


Fig. 24 *Stegocephalides attingens*, female (8mm) cotype.

ST7), ST 1 conspicuously enlarged, gap between ST 5 and ST 7 present; ST A present, located distally, part of first row; ST B-C present, part of second row, ST D absent; inner plate without a well developed shoulder, setae pappose.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft absent; inner plate setae row A covering the entire margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally pappose, distally with cusps present; row C present; row D present, 1-3 long setae distally, setae with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distal inner margin weakly produced, dactylus distally simple (pointed); inner plate with 2 nodular; medial setae-row present, reduced to one or two setae but differentiated from distal row, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row present, setae not conspicuously large; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short, strongly curved upwards (hooks); inner setae-row present but strongly reduced, setae short simple and slender, proximally parallel to outer, distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical, right lobe not reduced, left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods covered with simple setae. Coxae 1-3 contiguous.

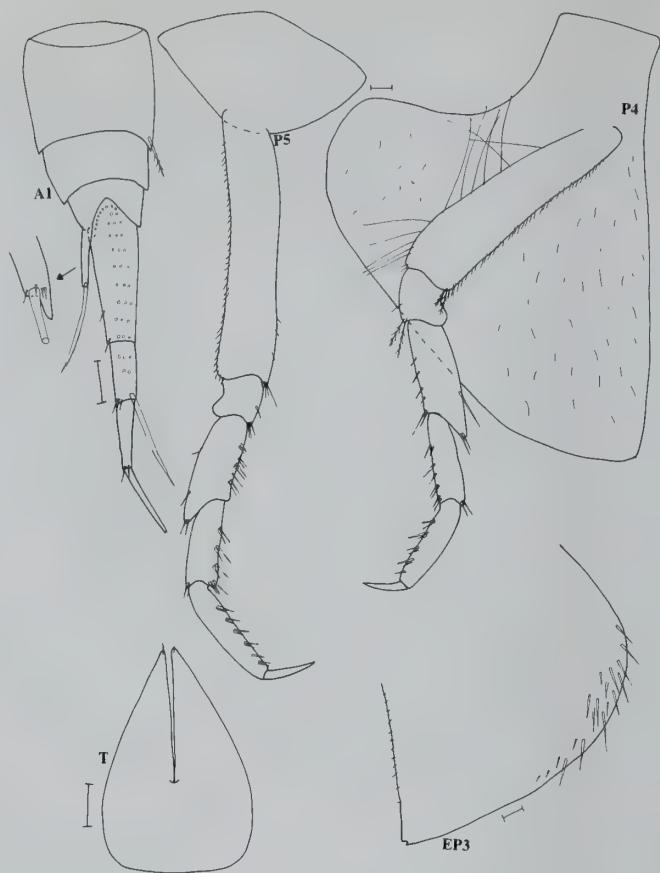


Fig. 25 *Stegocephalides attingens*, female (8mm) cotype.

Pereopod 1 coxa deeper than basis; propodus subovate.

Pereopod 2 general appearance like pereopod 1; ischium not elongate, ratio length:breadth not exceeding 1.5; ischium distal posterior margin plumose setae present; propodus subrectangular; ischium absent.

Pereopod 4 coxa posteroventral lobe large, reaching about the base of the 7th pereon segment; basis anterior margin without long setae, posterior margin with long setae, plumose setae on distal anterior margin, no plumose setae on distal posterior margin; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly unexpanded, with a row of long plumose setae present.

Pereopod 7 basis anterior margin straight, distally pointed and acute, with medial row of long setae.

Oostegites on pereopods 2-5, but strongly reduced on pereopod 2. Gills on pereopods 2-7.

Pleonites 1-3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 absent. Uropod 1 peduncle longer than rami, outer ramus as long as inner. Uropod 2 peduncle longer than rami, outer ramus shorter than inner. Uropod 3 peduncle longer than half the length of rami, outer ramus 1-articulate, outer ramus longer than inner.

Telson longer than broad, longer than peduncle uropod 3, cleft, apically pointed, submarginal setae on apex of each lobe.

MALE. Pereopod 2 propodus larger in males than in females. Urosome ordinary (similar to females).

REMARKS. The distally acute basis on pereopod 7 is a character state only shared with *Stegocephaloides auratus* (Sars, 1883), but S.

*attingens* is separated from the latter species by the shape of coxa 4 (*S. auratus* has a very deep coxa with the lower margin straight, whereas in *S. attingens* coxa 4 is not as deep and the lower margin is curved), by the strongly reduced oostegite on pereopod 2, and by article 4 on antenna 2 being almost as long as article 5.

***Stegocephaloides australis* K.H. Barnard, 1916**

(Figs 26–28)

*Stegocephaloides australis* K.H. Barnard 1916: 129

? *Stegocephaloides australis* Griffiths 1974: 324

? *Stegocephaloides australis* Griffiths 1975: 167

Non *Stegocephaloides australis* Ledoyer 1986: 962

MATERIAL EXAMINED. Syntypes, BMNH 1928.4.13.45–48; 4 females (6–8 mm), Cape Point, South Africa, 110–200m.

DISTRIBUTION. Endemic to South Africa.

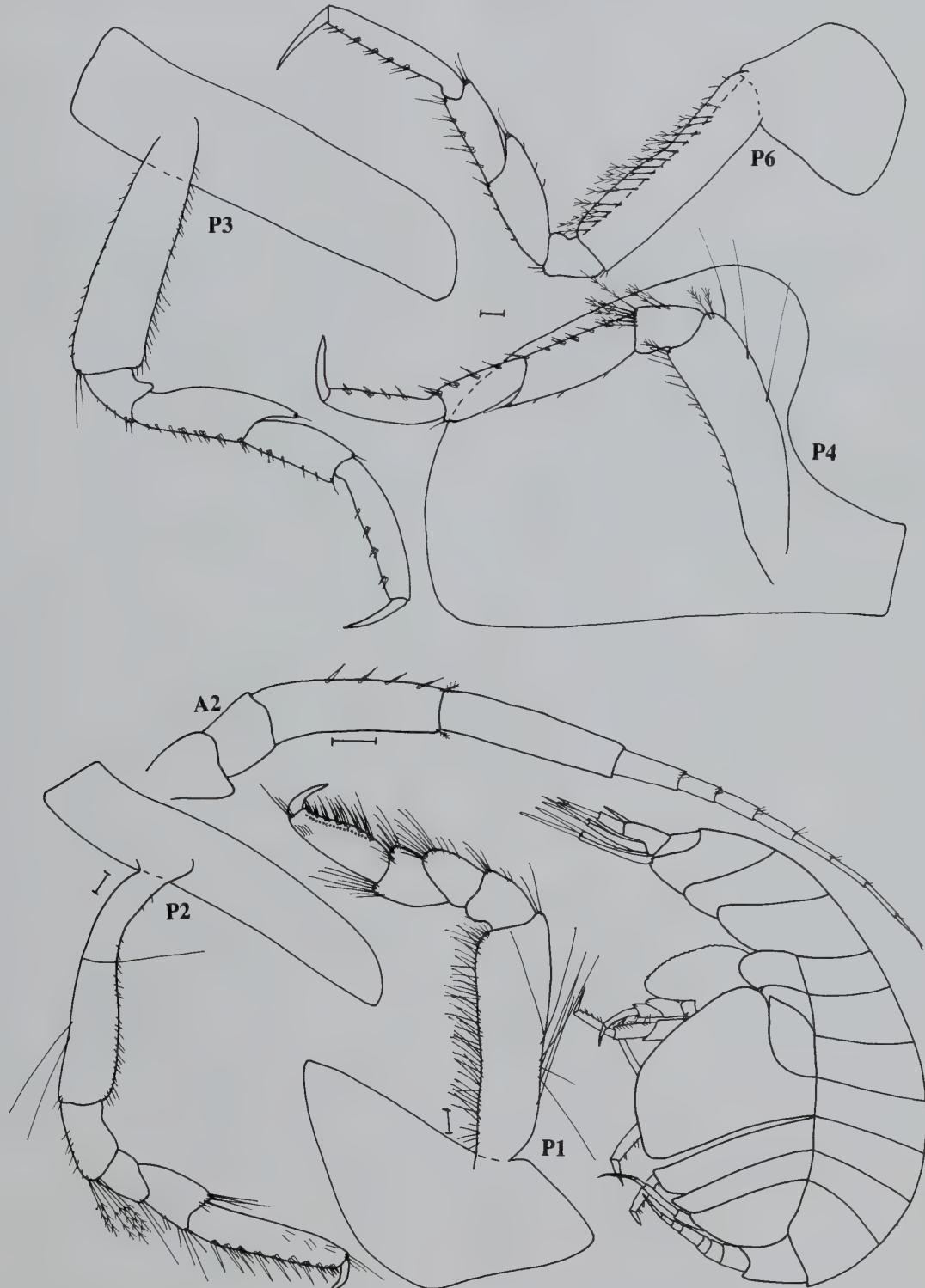


Fig. 26 *Stegocephaloides australis*, female (7mm) cotype.

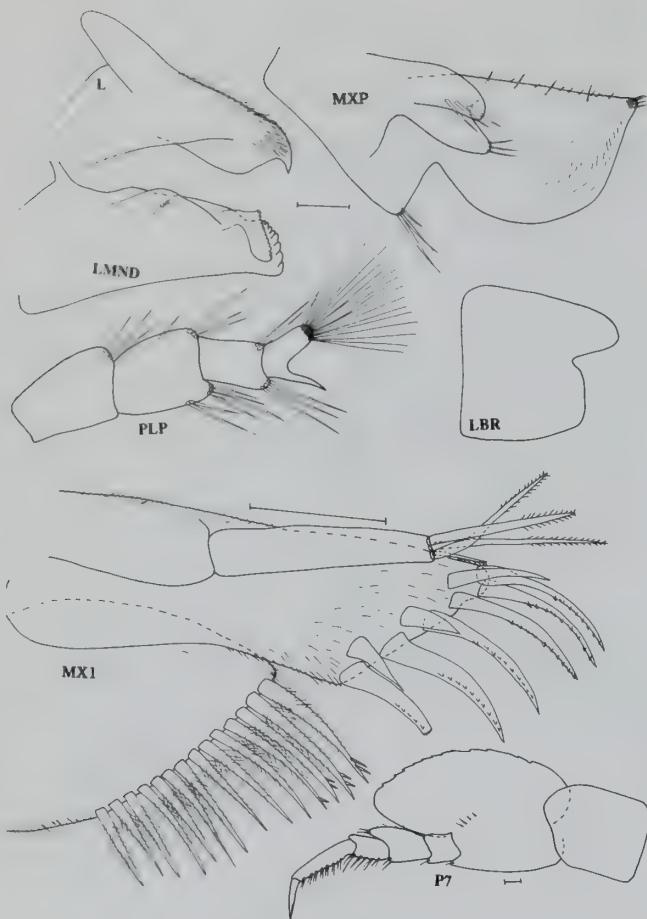


Fig. 27 *Stegocephaloides australis*, female (7mm) cotype.

**DESCRIPTION.** Biology: not pelagic, otherwise unknown.

Rostrum very small.

Antennae short. Antenna 1 equal to antenna 2; flagellum 5-articulate; accessory

flagellum article 2 absent. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 as long as article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced.

Mouthparts not elongate or pointed.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in a pseudocrown, ST first row with 6 setae (ST1–5, ST7), ST 1 conspicuously enlarged, gap between ST 5 and ST 7 present; ST A present, located distally and part of first row, ST B present, part of second row, ST C present, ST D absent; inner plate with a weakly developed shoulder, setae pappopectinate.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally pappose, distally with cusps present; row C present; row D present, expanded, row elongated towards and beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distal inner margin weakly produced, dactylus distally cleft with one pointed and one heavily setose part; inner plate with 2 nodular setae; medial setae-row

present, reduced to one or two setae but differentiated from distal row, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row present, setae not conspicuously large; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short, strongly curved upwards (hooks); inner setae-row present but strongly reduced, setae short simple and slender, proximally parallel to outer row and distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical, right lobe not reduced, left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subrectangular.

Pereopod 2 general appearance like pereopod 1, ischium not elongate, ratio

length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe large, reaching about the base of the 7th pereon segment; basis anterior margin without long setae, posterior margin with long setae, plumose setae on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin present.

Pereopod 6 basis posteriorly expanded, expansion rudimentary, with a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, with a medial row of short and robust setae.

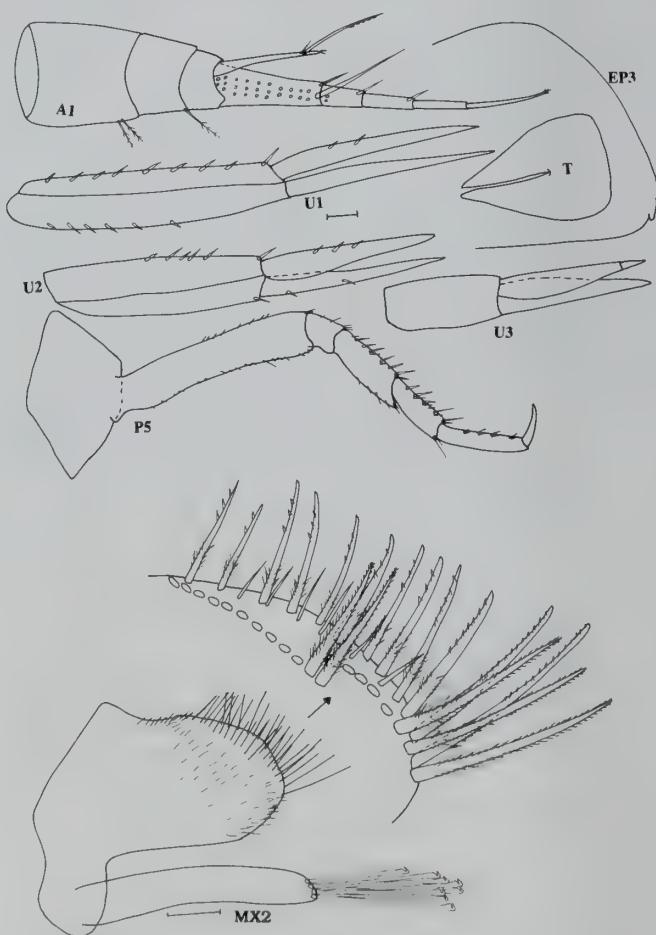


Fig. 28 *Stegocephaloides australis*, female (7mm) cotype.

Oostegites on pereopods 2–5. Gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 absent. Uropod 1 peduncle longer than rami, outer ramus as long as inner. Uropod 2 peduncle longer than rami, outer ramus as long as inner. Uropod 3 peduncle longer than half the length of rami, outer ramus 2-articulate, outer ramus as long as inner.

Telson longer than broad, longer than peduncle uropod 3, cleft, apically pointed, no submarginal setae on apex of each lobe.

MALE. Unknown.

**REMARKS.** This species is distinguished from all other stegocephalid species by the very peculiar dactylus on its maxilliped palp (see figure 27).

### *Stegocephaloides calypsonis* sp. nov.

(Figs 29–30)

**MATERIAL EXAMINED.** Holotype, female, 4 mm, BMNH 1992:1483:17, 10°38'N 65°32'W, 1400m, Calypso exp 7<sup>th</sup>, October 1979. Paratypes, 18 specimens, BMNH 1992:1483:17 (details, as above). Additional material: BMNH 1992:1484:15, 11 specimens, 10°31'N 64°45'W, 1300m, Calypso exp. 5<sup>th</sup> October 1979

**DISTRIBUTION.** Known only from the type locality.

**DESCRIPTION.** Biology: not pelagic, otherwise unknown.

Rostrum very small.

Antennae elongate. Antenna 1 longer than antenna 2; flagellum 6-articulate; accessory flagellum article 2 present. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3

short, about as long as broad; article 4 shorter than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced.

Mouthparts not elongate or pointed.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in a pseudocrown, ST first row with more than 6 setae (ST1–5 expanded, ST7), ST 1 conspicuously enlarged, gap between ST 5 and ST 7 absent; ST A present, located distally and part of first row, ST B present, part of second row, ST C present, ST D absent; inner plate without or with a weakly developed shoulder, setae pappose.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally pappose, distally with cusps present; row C present; row D present, expanded, row elongated towards and beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distally unproduced, dactylus distally simple (pointed); inner plate with 1 nodular setae; medial setae-row present, reduced to one or two setae but differentiated from distal row, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row present, setae not conspicuously large; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short and straight; inner setae-row present but strongly reduced, setae short and simple, proximally parallel to outer and distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical; right lobe not reduced; left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length:breadth exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe medium sized, not reaching the base of the 7<sup>th</sup> pereon segment; basis anterior margin without long setae, posterior margin with long setae present, no plumose setae on distal anterior and posterior margins; ischium without plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly unexpanded, without a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, no medial row of setae.

Oostegites on pereopods 2–5. Gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 absent. Uropod 1 peduncle longer than rami, outer ramus shorter than inner. Uropod 2 peduncle shorter than rami, outer ramus shorter than inner. Uropod 3 peduncle longer than half the length of rami, outer ramus 2-articulate, outer ramus shorter than inner.

Telson longer than broad, as long as peduncle uropod 3, cleft, apically rounded, no submarginal setae on apex of each lobe.

MALE. Pereopod 2 propodus larger in males than in females. Urosome ordinary (similar to females).

**REMARKS.** *Stegocephaloides calypsonis* is a rather small species, but with somewhat elongate appendages (antennae and pereopods). The arrangement of ST on maxilla 1 is similar to that found in *S. christianiensis* (Boeck, 1871), but the presence of a second article on outer ramus of uropod 3 and the rounded lower margin of coxa 4 indicate some relationship with *S. attingens* (outer ramus articulation absent, but with rounded coxa), *S. boxshalli* (see below) and *S. camoti* (Barnard, 1967).

**ETYMOLOGY.** Named after the French oceanographic vessel 'Calypso' from which the material was sampled. Galan (in his unpublished 1984 Ph.D. thesis) originally used the name *calypsae*, but this is here emended to the grammatically more correct *calypsonis*.

### *Stegocephaloides boxshalli* sp. nov.

(Figs 31–33)

*Stegocephaloides attingens* K.H. Barnard 1932: 131 (1 out of 4 specimens only)

**MATERIAL EXAMINED.** Holotype, SAM A43988, male, Cape Point 20<sup>th</sup> of August 1903.

Paratypes, SAM A43988, 3 specimens. Additional material: BMNH 1928.4.13.41–44, female ~7mm: Cape Point, South Africa, 500–1000m.

**DISTRIBUTION.** Known only from Cape Point, South Africa.

**DESCRIPTION.** Biology: not pelagic, otherwise unknown.

Rostrum very small.

Antennae short. Antenna 1 longer than antenna 2; flagellum 5-articulate; accessory flagellum, article 2 present. Antenna 2 peduncle (articles 3–5) as long as flagellum; article 3 short, about as long as broad; article 4 longer than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced.

Mouthparts not elongate or pointed.

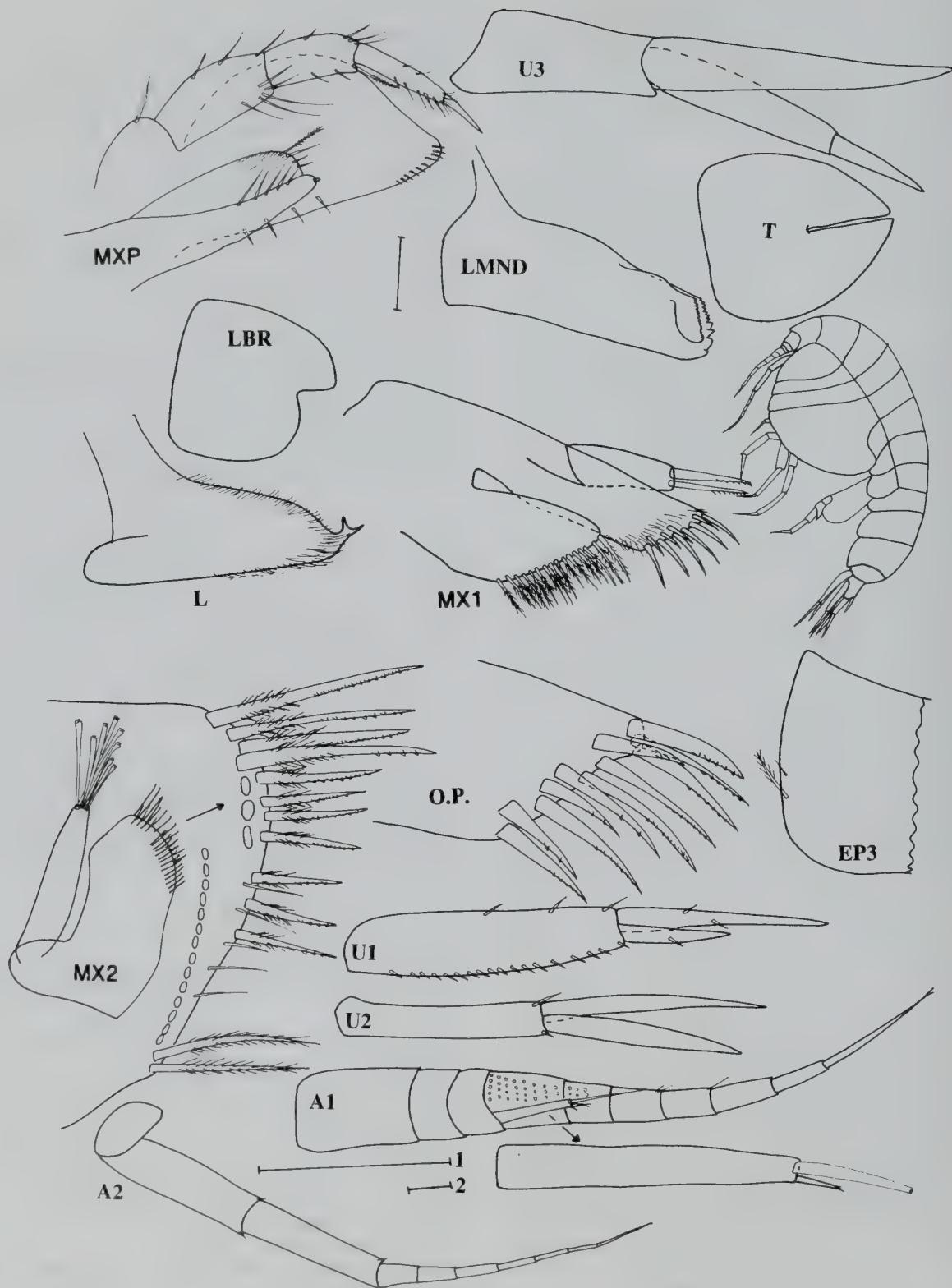
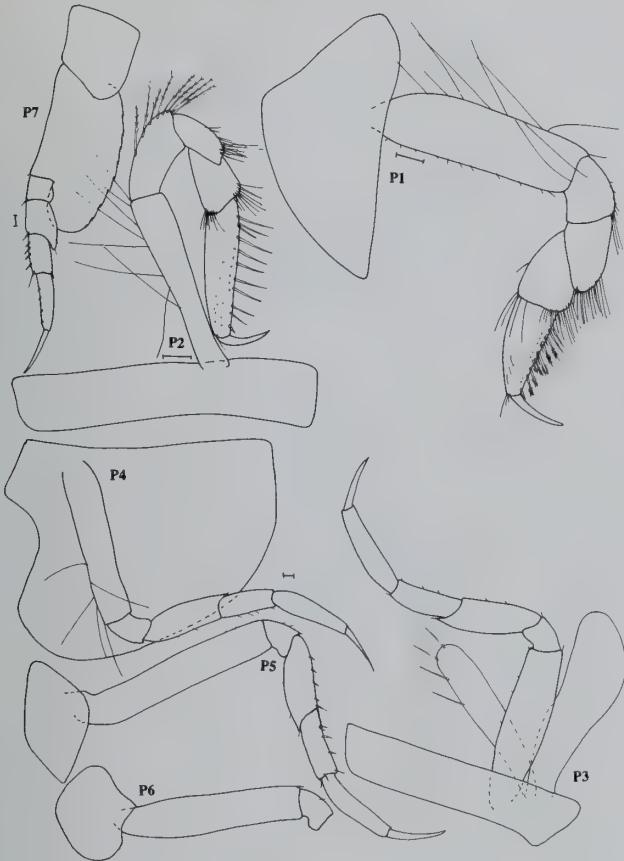


Fig. 29 *Stegocephaloides calypsonis* sp.nov., holotype.



**Fig. 30** *Stegocephaloïdes calypsonis* sp.nov., holotype.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in two parallel rows, first marginal and second submarginal, ST first row with 7 setae (ST1–5, ST7 and an additional ST located medially on outer plate), ST 1 ordinary (similar to ST 2–4), gap between ST 5 and ST 7 present; ST A–C, part of second row, ST D absent; inner plate with a well developed shoulder, setae pappopectinate.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally simple, distally with cusps present; row C present; row D present, expanded and elongated beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distal inner margin weakly produced, dactylus distally simple (pointed); inner plate with 2 nodular setae; medial setae-row absent, distal setae-row present, setae simple; inner setae-row present, row reduced to one or two setae, setae not conspicuously large; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short and strongly curved upwards (hooks); inner setae-row present but strongly reduced, setae short simple and slender, proximally parallel to outer and distally transverse; distal setae-group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical; right lobe not reduced; left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods covered with very short setules. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1, ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subovate, palm absent.

Pereopod 4 coxa posteroventral lobe large, reaching about the base of the 7<sup>th</sup> pereon segment; basis anterior margin without long setae, posterior margin with long setae, no plumose setae on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion rudimentary, with a row of long plumose setae.

Pereopod 7 basis anterior margin straight, distally rounded, with a medial row of short and robust setae.

Oostegites on pereopods 2–5. Gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus longer than inner. Uropod 2 unknown. Uropod 3 peduncle longer than rami, outer ramus 2-articulate, outer ramus shorter than inner.

Telson as long as broad, longer than peduncle uropod 3, cleft, apically rounded, no submarginal setae on apex of each lobe.

**MALE.** Pereopod 2 propodus larger in males than in females. Urosome ordinary (similar to females).

**REMARKS.** All five specimens were unfortunately lost in the mail after examination of the material, but before the description of the species was entirely finished. Four slides made from the holotype represent the only remaining material. Thus figures of uropod 2, epimeral plate 1 & 2 and habitus are not available.

The present species has some affinities to *S. attingens* (see above), reflected in the fact that all five specimens registered for this species had initially been identified as *S. attingens* (indeed, the one specimen identified by K.H. Barnard (1932) was among the type material of *S. attingens*). The two species are, however, separated by the basis of pereopod 7 (*S. boxshalli* is not pointed distally), by uropod 3 (*S. boxshalli* has a 2-articulate outer ramus) and by the shorter and more rounded telson of *S. boxshalli*. Furthermore, *S. boxshalli* can be separated from all other stegocephalid species by the presence of an additional ST on the outer margin of maxilla 1 outer plate.

**ETYMOLOGY.** The present species is named after Prof. Geoff Boxshall (Natural History Museum in London) for his support and help with the first authors' work on his Ph.D. thesis.

#### *Stegocephaloïdes ledoyerii* sp. nov.

(Figs 34–36)

*Stegocephaloïdes australis* Ledoyer 1986:962 (non *S. australis* K.H. Barnard)

**MATERIAL EXAMINED.** Holotype, SAM A15598, female 8mm. 27°59.5'S 32°40.8'E, collected 22<sup>nd</sup> May 1976. Additional material: 14 specimens identified as *S. australis*, see Ledoyer 1986:962.

**DISTRIBUTION.** Known from South Africa and Madagascar.

**DESCRIPTION.** Biology: not pelagic, otherwise unknown.

Rostrum very small.

Antennae short. Antenna 1 shorter than antenna 2 and longer than antenna 2; flagellum 6-articulate; accessory flagellum article 2 present. Antenna 2 peduncle (articles 3–5) longer than flagellum; article 3 short, about as long as broad; article 4 shorter than article 5.

Epistome curved (convex) and smooth; epistomal plate (medial keel) not produced.

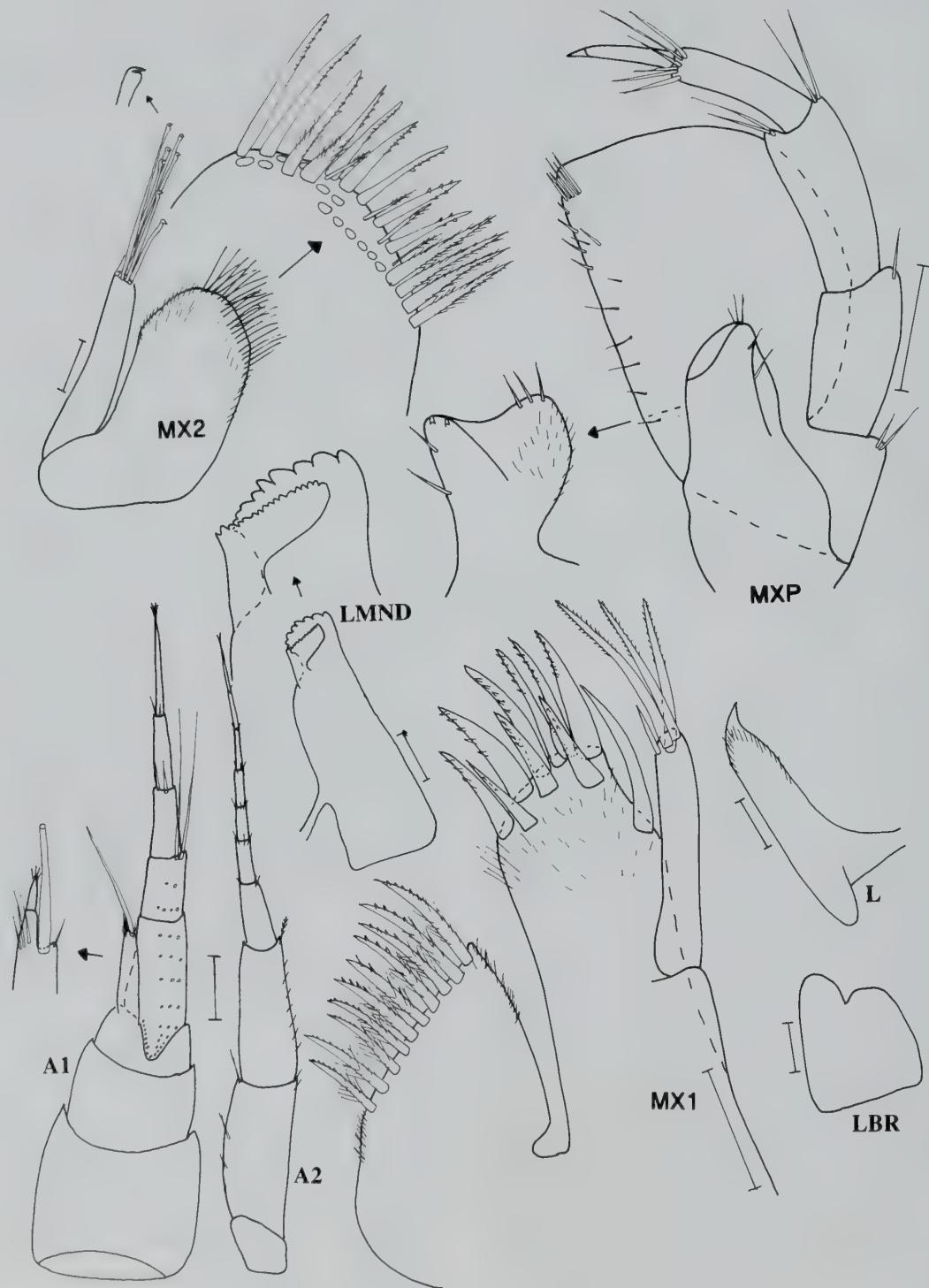
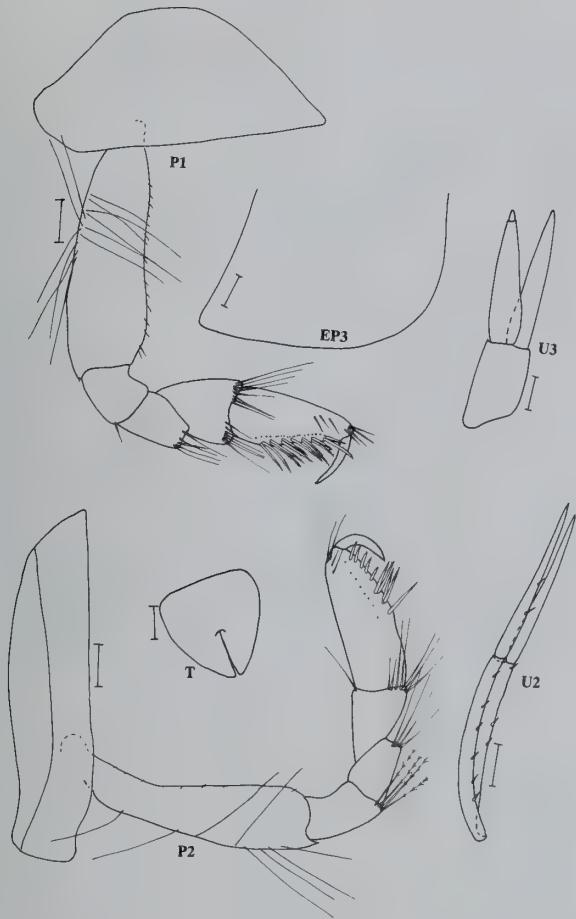


Fig. 31 *Stegocephaloïdes boxshalli* sp.nov., holotype.



**Fig. 32** *Stegocephaloïdes boxshalli* sp.nov., holotype.

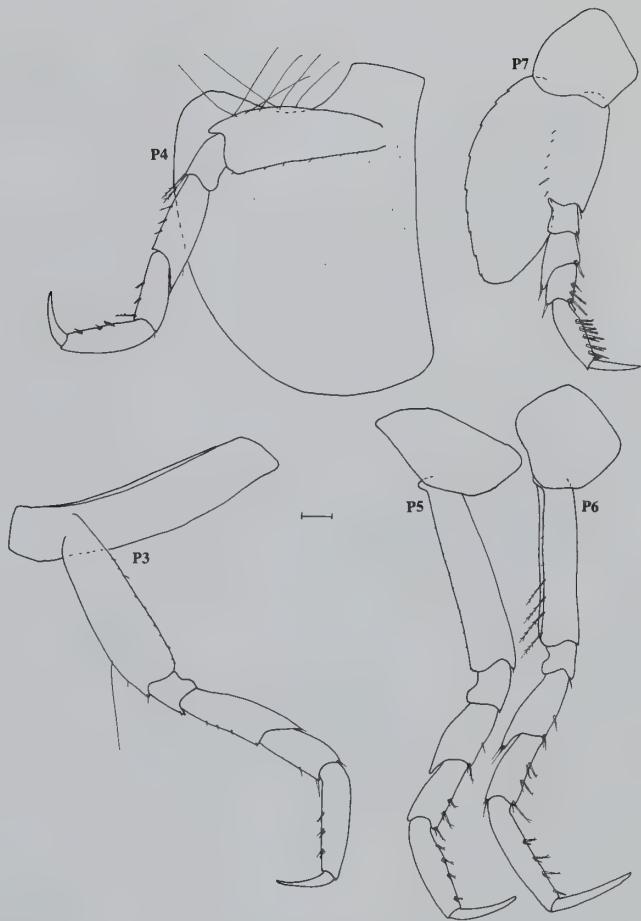
Mouthparts not elongate or pointed.

Mandible incisor lateral; incisor toothed; left lacinia mobilis present, powerful, laterally expanded, not conical.

Maxilla 1 palp 1-articulate, rectangular, apex not reaching beyond outer plate; outer plate distally rectangular; ST in a pseudocrown, ST first row with 6 setae (ST1–5, ST7), ST 1 conspicuously enlarged; ST A present; located distally and part of first row, ST B–C present, part of second row, ST D absent; inner plate with a weakly developed shoulder, setae pappopectinate.

Maxilla 2 gaping and geniculate, outer plate setae with distal hooks present, distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B, row A setae pappopectinate; row B setae proximally pappose, distally with cusps present; row C present; row D present, expanded and elongated beyond row A, with many small cusps distally.

Maxilliped palp 4-articulate, article 2 distally produced, distal inner margin weakly produced, dactylus distally simple (pointed); inner plate with 2 nodular setae; medial setae-row present, reduced to one or two setae but differentiated from distal row, transverse, setae pectinate; distal setae-row present, setae simple; inner setae-row present, setae not conspicuously large; outer plate outer setae-row present, marginal, setae attached in a deep hollow, setae short and strongly curved upwards (hooks); inner setae-row present but strongly reduced, setae short, simple and slender, proximally parallel to outer and distally transverse; distal setae-



**Fig. 33** *Stegocephaloïdes boxshalli* sp.nov., holotype.

group present, setae attached in a deep hollow, setae short simple.

Labrum elongate; lobes asymmetrical, right lobe not reduced, left lobe reduced.

Labium distally narrowing.

Coxal plates and basis of pereopods smooth. Coxae 1–3 contiguous.

Pereopod 1 coxa deeper than basis; propodus subovate.

Pereopod 2 longer and thinner than pereopod 1, ischium not elongate, ratio length:breadth not exceeding 1.5, ischium distal posterior margin with plumose setae; propodus subrectangular, palm absent.

Pereopod 4 coxa posteroventral lobe large, reaching about the base of the 7th pereon segment; basis anterior margin without long setae, posterior margin with long setae, plumose setae on distal anterior margin, no plumose setae on distal posterior margin; ischium with plumose setae on posterior distal margin.

Pereopod 6 basis posteriorly expanded, expansion rudimentary, with a row of long plumose setae present.

Pereopod 7 basis anterior margin straight, distally rounded, with a medial row of short and robust setae.

Oostegites on pereopods 2–5. Gills on pereopods 2–7.

Pleonites 1–3 dorsally smooth.

Urosome: articulation between urosome segments 2 and 3 present. Uropod 1 peduncle longer than rami, outer ramus as long as inner. Uropod 2 peduncle as long as rami, outer ramus shorter than inner.

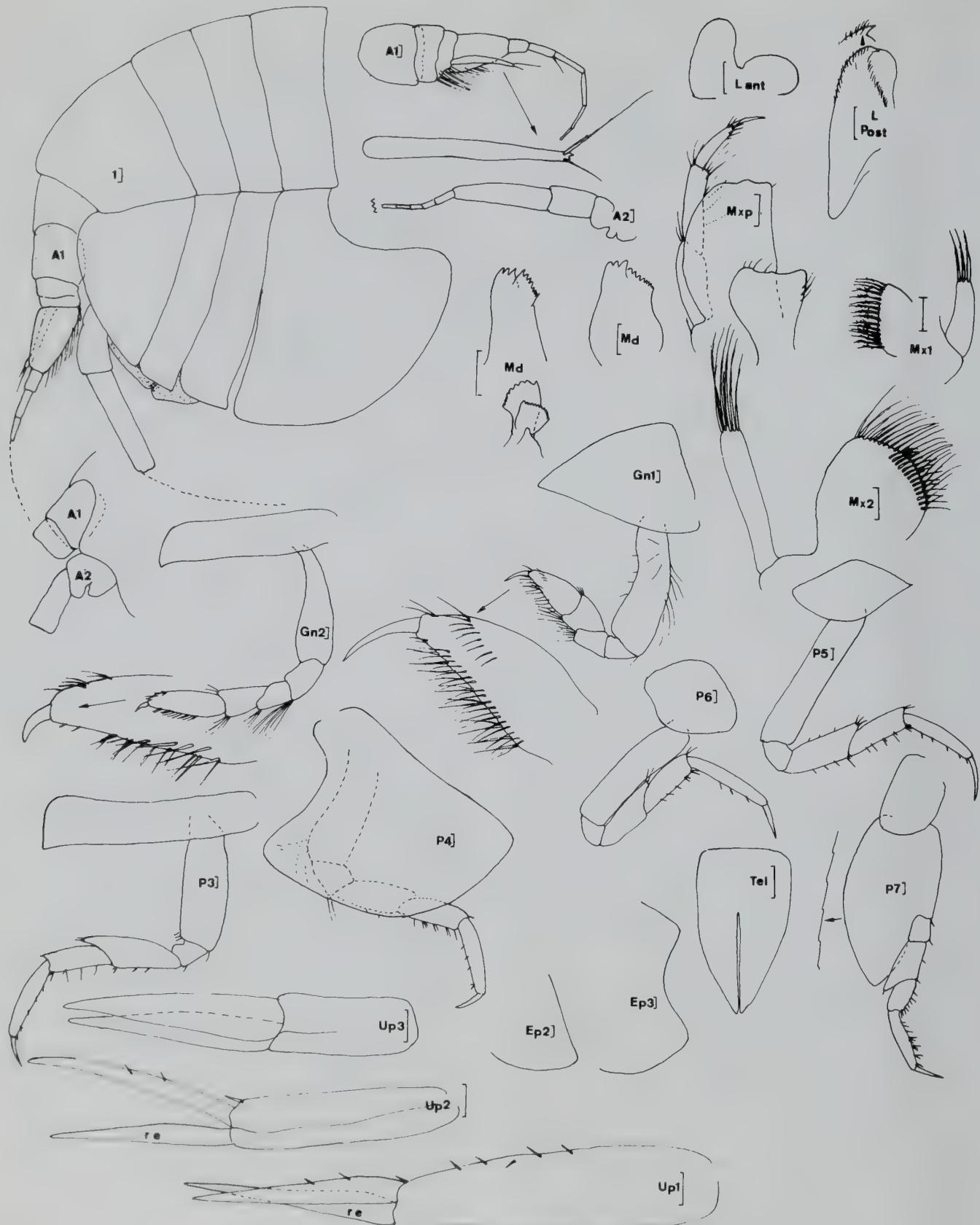


Fig. 34 *Stegocephaloides ledoyer sp.nov.*, from: Ledoyer 1986:963, fig.379 '*Stegocephaloides australis*'.

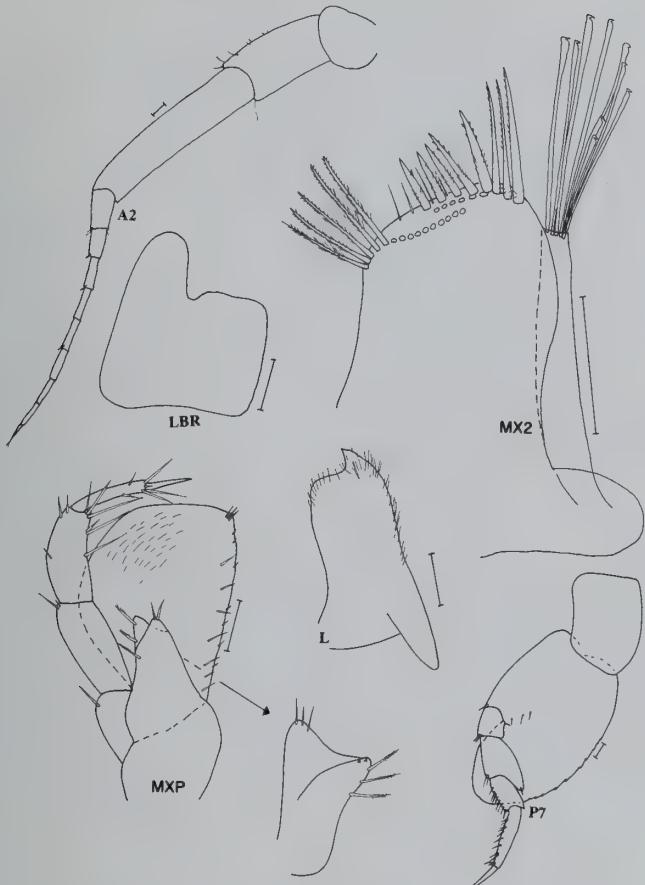


Fig. 35 *Stegocephaloides ledoyerri* sp.nov., holotype.

Uropod 3 peduncle longer than half the length of rami, outer ramus 1-articulate, outer ramus longer than inner.

Telson longer than broad, longer than peduncle uropod 3, cleft, apically pointed, no submarginal setae on apex of each lobe.

**MALE.** Pereopod 2 propodus larger in males than in females. Urosome ordinary (similar to females).

**REMARKS.** The present species is distinguished from all other *Stegocephaloides* species by the combination of a distally rounded basis of pereopod 7 and a short article 4 on the peduncle of the second antenna (about 1/2 the length of article 5).

**ETYMOLOGY.** This species is named after Prof. M. Ledoyer, who first described material of this species (Ledoyer 1986:962, identified as *Stegocephaloides attingens*).

## DISCUSSION

The present paper is part of series that will lead to a complete revision of the family (Berge & Vader, in press.), that will also include a cladistic analysis of all its species. Thus, the species treated herein are described without any further reference to their phylogenetic relationships. Consequently, some of these species may, in future, be transferred to different genera.

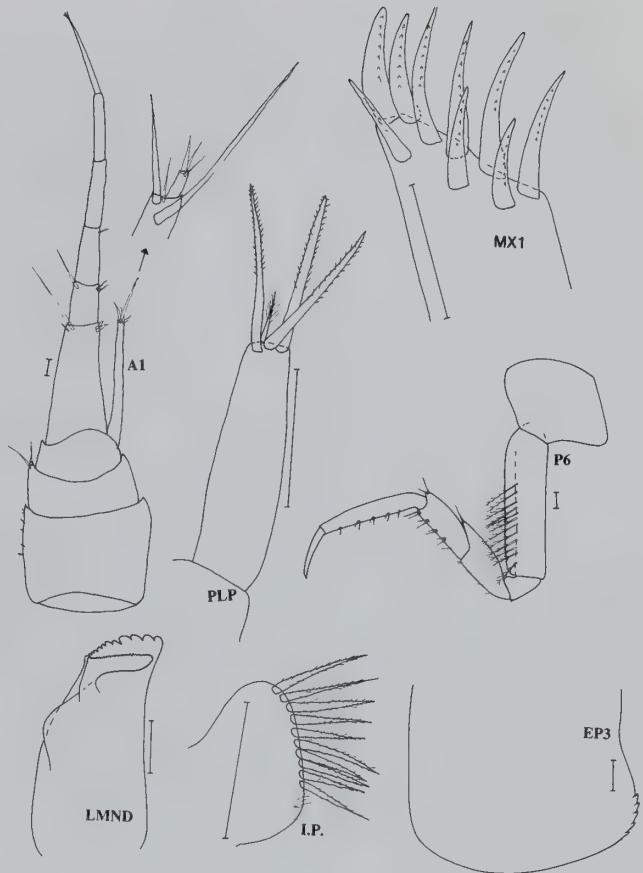


Fig. 36 *Stegocephaloides ledoyerri* sp.nov., holotype.

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# The genus *Ischioscia* Verhoeff, 1928 in Venezuela, with the description of six new species (Crustacea, Oniscidea, Philosciidae)

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## CONTENTS

Introduction .....	137
Materials and Methods .....	137
Systematics .....	138
<i>Ischioscia variegata</i> (Dollfus, 1893) .....	138
<i>Ischioscia fasciifrons</i> sp. nov. .....	138
<i>Ischioscia hirsuta</i> sp. nov. .....	143
<i>Ischioscia colorata</i> sp. nov. .....	143
<i>Ischioscia pariae</i> sp. nov. .....	152
<i>Ischioscia guamae</i> sp. nov. .....	157
<i>Ischioscia trifasciata</i> sp. nov. .....	157
Discussion .....	166
Acknowledgements .....	167
References .....	167

**SYNOPSIS.** Terrestrial isopods (Oniscidea) collected in Venezuela in 1998 revealed plentiful material of the philosciid genus *Ischioscia*. This genus was, until very recently, represented in Venezuela by only a single species, *I. variegata* (Dollfus, 1893). The examination of the new samples lead to the description of six new species, all confined to small areas within Venezuela; five of which are closely related to *I. variegata*. These species are described in the present paper and the biogeography of the genus is discussed for Venezuela. The characters, which are important for reconstructing the phylogeny are presented and the relationships of the species are also discussed.

## INTRODUCTION

The genus *Ischioscia* Verhoeff, 1928 was one of the first genera of philosciid Oniscidea described from South America (Verhoeff 1928). It was instituted for a species from Venezuela, *I. lobifera* Verhoeff, 1928, which is now considered to be a junior synonym of *I. variegata* (Dollfus, 1893), a species reported from several localities in northern South America (Leistikow 1997). The genus comprises the largest species of terrestrial Isopoda in South America, with *I. variegata* reaching a body length of about 15 mm. Beside this species, several others are reported from the Peruvian and Brazilian Amazon region (Lemos de Castro 1955, Schmalfuss 1980), from Central America (van Name 1926, Arcangeli 1930, Leistikow 1997, 1999 and 2000) and even from the lesser Antilles (van Name 1936). The total number of nominal species now is 16, and it is likely that several others will be found when the vast Amazonas region is better explored. The number of known species increased in those regions where larger collections were made. For example, in Costa Rica, ten species have been discovered in the last decade. The samples from Venezuela dealt with in this study revealed the presence of six more species; most of them close to *I. variegata*, but quite distinct in several characters. Hence, several records of *I. variegata* may show

to belong to other species. The species of *Ischioscia* found in Venezuela are described in detail, the holotypes are deposited in The Natural History Museum, London for which the acronym BMNH is used below. Paratypes are deposited in The Natural History Museum, London, the Muséum d'Histoire Naturelle, Genève (MHNG), Staatliches Museum für Naturkunde, Stuttgart (SMNS), the museum of the University of Marcau, Venezuela (MUMV), and in the collection of the author. The new species belong to the *martinae-variegata*-group of species distributed in Central America and northern South America. Particularly five of the new species are forming a monophylum together with *I. variegata* and *I. panamensis*. They seem to be restricted to smaller areas in Venezuela, and their distribution is compared with those of other taxa.

## MATERIALS AND METHODS

Several samples of isopods preserved in 70% ethanol were examined. The samples were checked with a Wild stereoscope and in the case of new species a holotype was selected for preparation. Drawings were made using a camera lucida. Some specimens were dissected and the appendages were mounted on microscopic slides in glycerine gelatine,

the appendages were then drawn using a camera lucida including drawings of the new species. The types selected for museum storage are preserved in 70% ethanol/5% glycerine.

## SYSTEMATICS

### *Ischioscia variegata* (Dollfus, 1893)

MATERIAL EXAMINED. 19 males, 11 females (with marsupium), 11 females/immature: Parque Nacional El Avila 10°34.70'N 66°53.92'W, banana plantation, forest along brook, leg. C. Schmidt 10.3.1998; 3 males, 10 females (with marsupium), (MHNG); 8 females 11 immatures: 10°33.01'N 66°54.41'W Forest with Bamboo, *Heliconia* sp., *Ricinus* sp. among others, gas pipeline crossing under street, small river, under bamboo leaves on sand, gravel, leg. C. Schmidt 11.3.1998; 1 male: Aragua, Parque Nacional Henry Pittier, Mist forest near Estación Biológica Rancho Grande, between leaves of fallen bromeliad, leg. C. Schmidt 14.3.1998; 1 male, 1 females (with marsupium), 1 immature: Aragua, Parque Nacional Henry Pittier, street heading from Rancho Grande to sea shore, near Capilla Virgen del Carmen, Mist forest, brook with cascade, under moist leaf litter and stones, leg. C. Schmidt 15.3.1998; 1 male: Falcón, Parque Morrocoy, Península de Morrocoy, northern shore, Cueva del Indio (carstic cave with crushed ceiling, within detritus in small niches and edges of the rock, under stones on bottom, leg. C. Schmidt 18.03.1998; 3 males, 3 females (with marsupium), 6 females: Sierra de San Luis, 11°07.35'N 69°40.74'W opposite to Cueva San Luis, forest with almost dried out brook emerging from cave, stones litter, Bombacaceae, Piperaceae, mango-trees, under logg, leg. C. Schmidt 20.3.1998; 2 males, 1 females (with marsupium), 2 females: Curimagua 11°11.61'N 69°39.96'W track to Cueva de Lugo, banana plantation, under loggs, leg. C. Schmidt 21.3.1998; 1 female, 3 immatures: Curimagua, Cueva de Lugo 11°11.90'N 69°39.88'W carstic cave without water, moist bottom, at the entrance under stones, leg. C. Schmidt 21.3.1998; 4 males, 3 females (with marsupium), 6 females, 2 immatures: Cueva Acurite 11°10.42'N 69°37.75'W carstic cave with water, surrounded by forest and banana plantation, at the entrance under stones and leaf litter, leg. C. Schmidt 21.3.1998; 3 males, 3 females, 1 immature: Eastern slope of Andes 'La Campana' 8°51.92'N 70°37.14'W 1500 m (+/- 200 m) moist forest (Araceae, Arecaceae, Melastomataceae, Orchidaceae) under leaf litter, leg. C. Schmidt 24.3.1998; 1 male, 1 female: Península de Paria, Puy Puy 10°42.00'N 62°58.05'W bay with sandy beach, coconut palms, surrounded by dry mountains, small westernmost bay, under loggs, coconuts and leaf litter, leg. C. Schmidt 29.3.1998; 1 males, 3 females (with marsupium), 11 females/immature: Península de Paria, Puy Puy 10°42.00'N 62°58.05'W bay with sandy beach, coconut palms, surrounded by dry mountains, forest at the edge of banana plantation east of bay, in leaf litter, leg. C. Schmidt 1.4.1998; 2 immature males, 1 female (with marsupium): Caripe, surroundings of Cueva del Guacharo 10°10.37'N 63°33.14'W moist forest, under rotting loggs and leaf litter along brook, leg. C. Schmidt 7.4.1998; 1 male: Península de Paria, southern shore of eastern part, 10°34.87'N 63°03.60'W, thermal well with thatched roof, uncovered near water edge; surrounded by meadows with cattle, leg. C. Schmidt 8.4.1998

### *Ischioscia fasciifrons* sp.nov.

Figs 1–4

MATERIAL EXAMINED. Holotype, male (body length 10 mm): Curimagua, 1250 m, under wood in the garden of a hotel, leg. C. Schmidt 21.03.1998.

## DESCRIPTION

**Colour.** Dorsum on a light umber ground colour patched with light spots and a darker medial band running down to the pleon, coxal plates with dark patches, on coxal plates VI and VII extensive dark areas. Cephalothorax with a dark band between the compound eyes on postfrons, profrons with a dark inverted Y covering lamina frontalis, extending ventrally.

**Cephalothorax.** Vertex flattened with few tricorn-like setae, compound eyes consisting of about 26 ommatidia arranged in four rows. Lamina frontalis and very faint linea supra-antennalis present, linea frontalis lacking (Fig. 1, Ct1).

**Pereon.** Cephalothorax set back into pereonite 1 coxal plates prominent, with sulcus marginalis, no gland pores or noduli laterales visible in light microscope, tegument smooth, bearing several slender tricorn-like setae, highest density along lateral and distal margins (Fig. 1, Cx3).

**Pleon.** Set apart from pereon, neopleurae of pleonites 3 to 5 prominent, pleotelson with concave lateral margin, as long as protopodites of uropods.

**Antennula.** Composed of three articles of subequal length, distal article pointed with several aesthetascs apically and along medial margin, caudal side of proximal article extended (Fig. 1, An1).

**Antenna.** Broken in the specimen examined, peduncular articles bearing tricorn-like setae (Fig. 1, An2).

**Mandible.** Pars intermedia with coniform setae, two penicils on left and one on right side, additional plumose seta proximally, molar penicil composed of about 7 branches (Fig. 2, Mdl/r).

**Maxillula.** Medial endite with two stout penicils apically and small subapical tip, lateral endite with 4+6 teeth apically, 3 of inner set deeply, two slightly cleft, slender subapical tooth and acute hyaline lobe caudally (Fig. 2, Mx1).

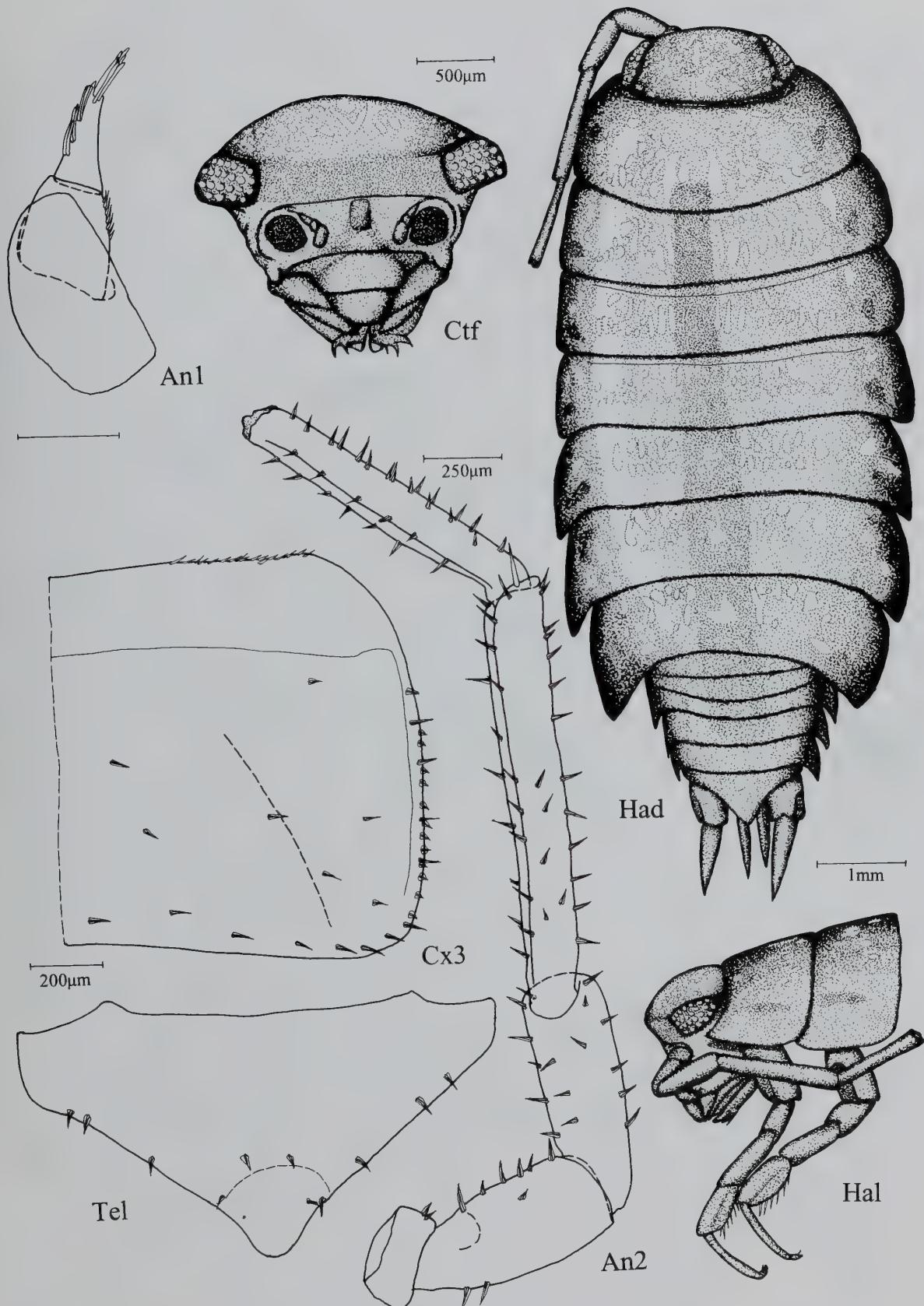
**Maxilla.** Both lobes covered with faint setation, medial trichiae stronger, lateral lobe slightly broader than medial, medial lobe apically cuspidate (Fig. 2, Mx2).

**Maxilliped.** Basipodite with plentiful cover of tricorn-like setae, sulcus lateralis present, endite caudally setose, rostrally with knob-like penicil, palp with proximal article bearing short and long seta, medial article with short proximal setal tuft, distal tufts slightly stalked (Fig. 2, Mxp).

**Pereopods.** Pereopods slender (Fig. 3, PE3–7; Fig. 4, PE1), carpus with antenna-grooming brush and ornamental sensory spine with hand-like apex (Fig. 3, Sc1), dactylus with long inner claw and simple dactylar seta, apically slightly tapered (Fig. 3, Dac). Sexual differentiation. Pereopod 1 and 2 carpus enlarged with setal field rostrally, enlargement not too prominent, pereopod 3 with a very small setal field on medio-proximal border of carpus and mediolateral margin of merus. Pereopod 6 ischium with a small depression rostrally near medial margin with sensory spine, pereopod 7 ischium with a slightly twisted medial margin, thus forming a groove rostrally, slight distal lobe with few trichiae.

**Pleopods.** Pleopod endopodites bilobate, exopodites with about 8 to 9 sensory spines laterally, medially with trichiae and minute pectinate scales, pleopod 5 with caudal creel of three rows of prominent pectinate scales, protopodite 3 to 5 with medial protrusion, less conspicuous on pleopod 4 and 5, rudimental epipodites on pereopod 1 to 4 (Fig. 4, PL1–5). Sexual differentiation. Male pleopod 1 exopodite triangular with lateral protrusion hardly set apart, incision merely a sinuosity, endopodite apically obtuse, with minute spines apically and lateral row of minute spines. Pleopod 2 exopodite elongate with about 12 sensory spines laterally, medially with minute pectinate scales, endopodite longer than exopodite, apex looking like a hypodermic needle.

**Uropod.** As in other species of the genus.



**Fig. 1** *Ischioscia fasciifrons* sp.nov. Holotype, male, 10 mm. An1 antenna; An2 antenna; Ctf cephalothorax in frontal view; Cx3 coxal plate 3; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

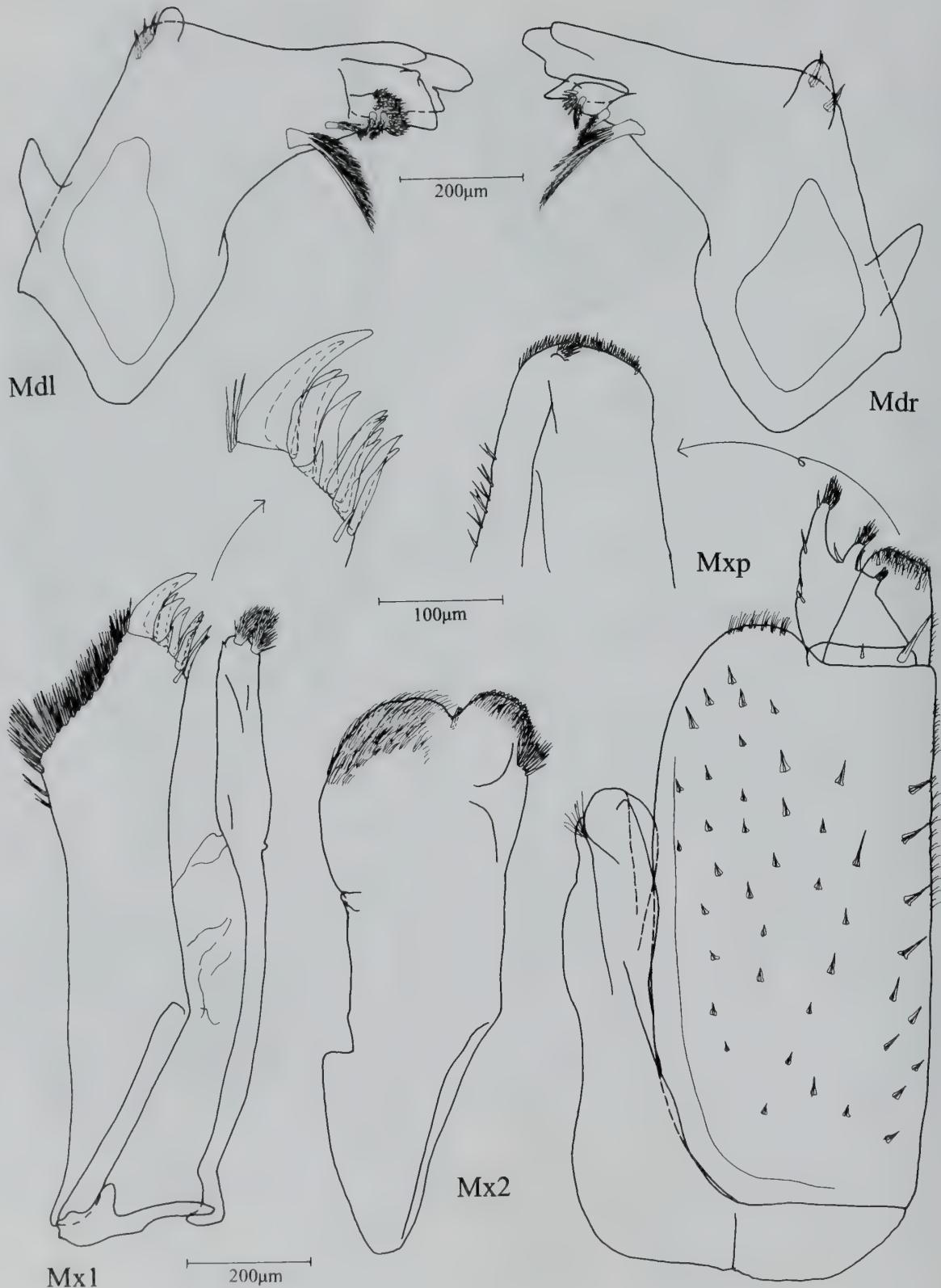
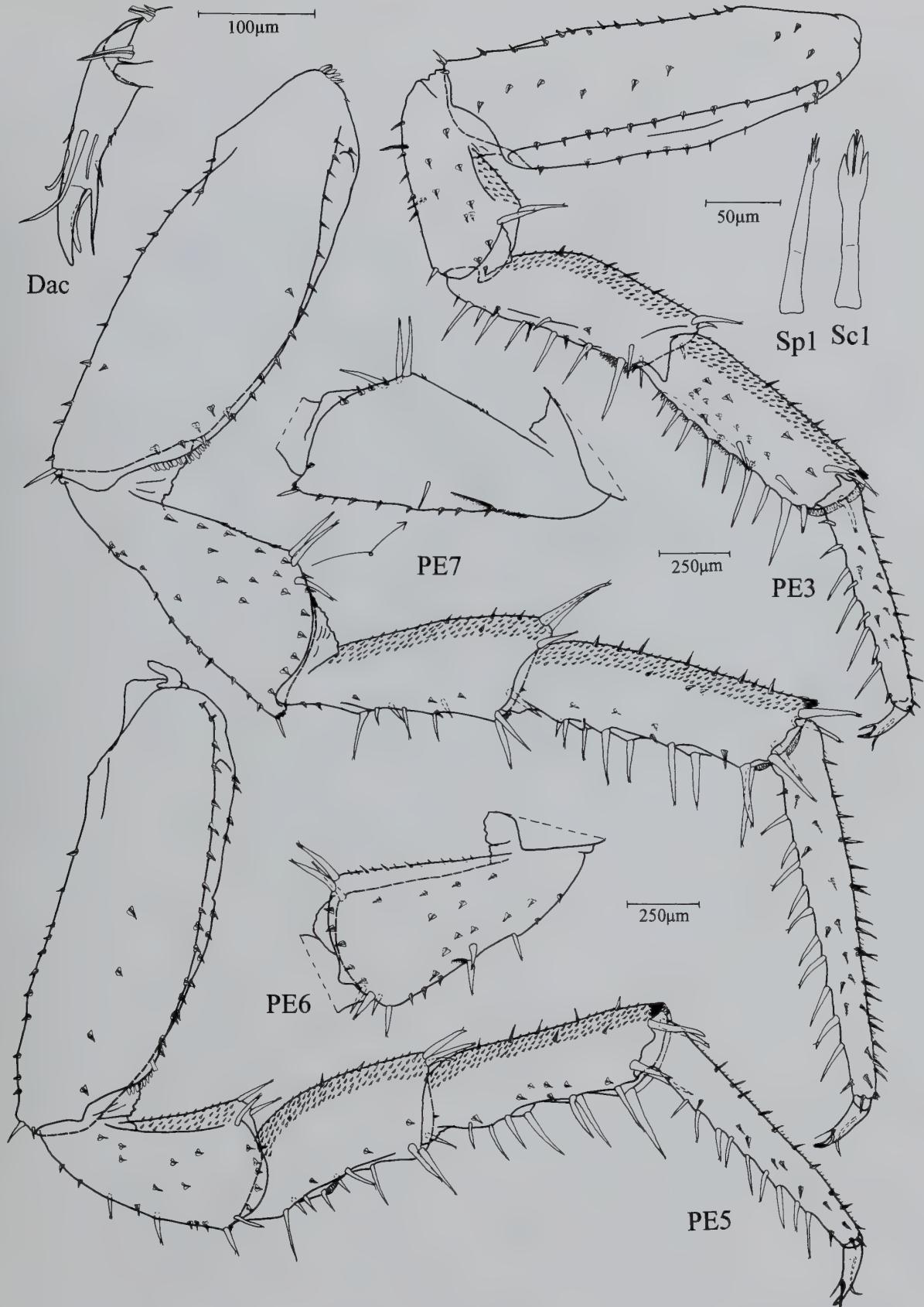


Fig. 2 *Ichthioscia fasciifrons* sp.nov. Holotype, male, 10 mm. Mdl/r left and right mandible; Mx1 maxillula with detail of apex of lateral endite in rostral view; Mx2 maxilla in caudal view; Mxp maxilliped, with detail of endite in rostral view.



**Fig. 3** *Ischiopsis fasciifrons* sp. nov. Holotype, male, 10 mm. Dac dactylus 1 in rostral view; PE3–7 pereopods 3 to 7 in caudal view, ischium 7 in rostral view; Sc1 ornamental sensory spine of carpus 1, Sp1 distalmost sensory spine of propus 1.

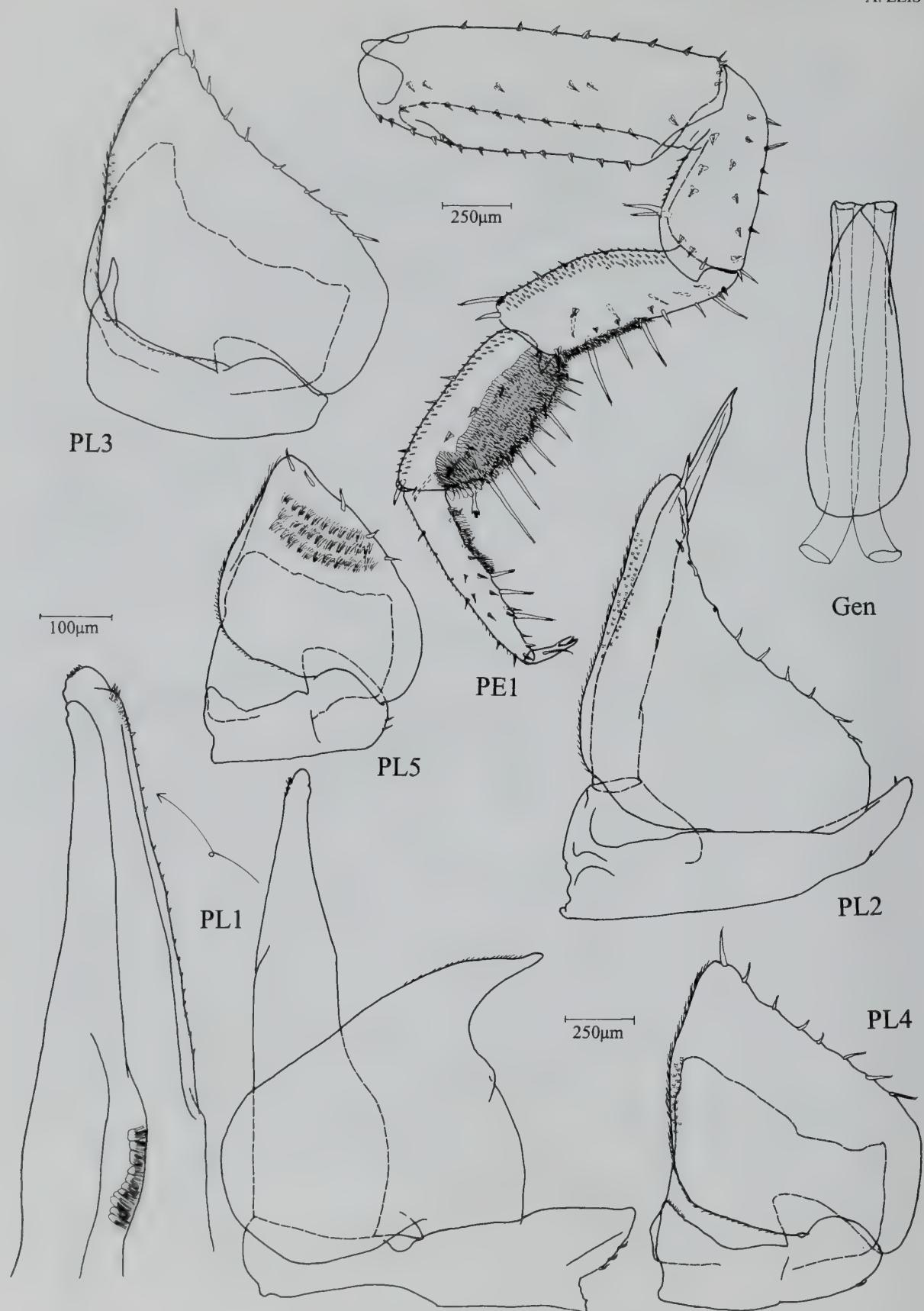


Fig. 4 *Ichiocera fascifrons* sp.nov. Holotype, male, 10 mm. Gen genital papilla; PE1 pereopod 1 in rostral view; PL1–5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

*Genital papilla.* Ventral shield slightly surpassing terminal spatula (Fig. 4, Gen).

**ETYMOLOGY.** The species name refers to the conspicuously darker profrons, compared to the colouration of the cephalothorax.

### *Ischioscia hirsuta* sp.nov.

Figs 5–8

**MATERIAL EXAMINED.** Holotype, male (body length 11mm): Andes, Mesa cerrada between La Puerta and Timotes, 9°00.26'N 70°44.20'W 1800 m (+/- 200 m, on the bank of a brook under stones and moist leaf litter, sugar cane, shrub with climbing plants, Polygonaceae, Poaceae, leg. C. Schmidt 23.03.1998; Paratypes: 14 males, 10 females (with marsupium), 6 females, 2 immatures: same data as holotype; 6 males, 19 females (with marsupium), 15 females/immatures: Andes, road from Timotes to Mérida, 8°53.72'N 70°47.99'W 3400 m (+/- 500 m), very steep northern slope, covered with Bryophyta, Pteridophyta, Poaceae, Ericaceae, between Bryophyta, leg. C. Schmidt 23.03.1998 (MNHG); 3 males, 2 females (with marsupium), 10 females, 2 immatures: Andes, 8°43.12'N 70°46.04'W, on the bank of a brook near cattle meadow, scrub with Asteraceae, *Rubus*, one specimen submerged, leg. C. Schmidt 24.03.1998

#### DESCRIPTION

*Colour.* Ground colour chestnut with many light markings on cephalothorax and pereonites, coxal plates of same colour, dark brown band in the medial line of each pereonite, pleon bearing some light spots.

*Cephalothorax.* Linea frontalis lacking, lamina frontalis and linea supra-antennalis prominent. Vertex smooth with plenty flagelliform tricorn-like setae, laterally protruding compound eyes composed of 22 ommatidia in four rows (Fig. 5, Ctf).

*Pereon.* Tegument smooth and shiny, bearing many flagelliform tricorn-like setae, coxal plates I to IV caudally rounded, coxal plates V to VII increasingly pointed, sulcus marginalis present, no gland pores nor noduli laterales discernible in light microscope at 400x magnification (Fig. 5, Cx4).

*Pleon.* Set back from pereon despite neopleurae of pleonite 3 to 5. Pleotelson rather pointed, lateral margins concave, some tricorn-like setae near the apex.

*Antennula.* Similar to other species of genus (Fig. 5, An1).

*Antenna.* Flagellum three-articulate, with proximal article longest, somewhat shorter than peduncular article 5, apical organ longer than distal article, length ratio of peduncular articles similar to next species (Fig. 5, An2).

*Mandible.* Pars intermedia bearing coniform setae and two penicils on left, one on right side, additional plumose seat proximally, molar penicil consisting of about 7 branches (Fig. 6, Mdl/r).

*Maxillula.* Medial endite with two stout penicils apically and a short subapical tip, lateral endite with 4+6 teeth apically, 5 of inner set cleft, on caudal side, a hyaline lobe, stalk and two subapical teeth present (Fig. 6, Mx1).

*Maxilla.* Lateral lobe slightly broader than medial, bearing faint trichiae and pectinate scales, lateral area of rostral side seta-free, medial one densely covered with trichiae, medial setal tuft present, apically cuspidate (Fig. 6, Mx2).

*Maxilliped.* Basipodite with sulcus lateralis and many tricorn-like setae, palp with proximal setal tuft small, medial one stalked, as prominent as distal one, proximal article bearing a long and a very short seta, endite covered with trichiae, on rostral side with knob-like penicil (Fig. 6, Mxp).

*Pereopods.* Slender with many sensory spines on medial margin (Fig. 7, PE1–7), pereopod 1 carpus with antenna-grooming brush,

propus with antagonistic device, dactylus with long inner claw, dactylar seta apically plumose (Fig. 8, Dac). Sexual differentiation. Pereopods 1 to 3 with subequally enlarged carpus and setal field rostrally, merus 1 to 3 with medial setal field, propus 2 with small setal field. Pereopod 7 ischium with prominent setal brush on proximal half medially, very long trichiae inserted on the more rostral surface, distally connected with a small cuticular clasp, bordered by small depressions, caudally a row of small trichiae, medio-distally with a lobe covered with short trichiae, laterally two sensory spine, third spine more caudodistally, basis 7 medio-distally with setal field around distal sensory spine.

*Pleopods.* Pleopod endopodites slightly bilobate, exopodites with about 10 sensory spines laterally, pleopod 5 with creel of three rows of pectinate scales caudally, protopodites 3 to 5 with medial protrusion, protopodites 4 and 5 lacking rudimental epipodite (Fig. 8, PL1–5). Sexual differentiation. Male pleopod 1 exopodite triangular with rounded medial edge, lateral point small, incision proximally bordered by small protrusion, endopodite slender with lateral row of spines, apex with prominent tooth rostrally, faint trichiae caudally, medial protrusion subapically. Pleopod 2 exopodite as in other species, with minute pectinate scales medially, endopodite pointed. *Uropod.* As in other members of the genus.

*Genital papilla.* Ventral shield slender, terminal spatule not surpassing ventral shield (Fig. 8, Gen).

**ETYMOLOGY.** The species is named for its long tricorn-like setae on the pereonites, giving it a hairy appearance.

### *Ischioscia colorata* sp.nov.

Figs 9–12

**MATERIAL EXAMINED.** Holotype, male (body length 14 mm): Aragua, Parque Nacional Henri Pittier, Road from Rancho Grande to the seaside, near Capilla Virgen del Carmen, mist forest, near brook and cascade in moist leaf litter and under stones, leg. C. Schmidt 14.03.1998. Paratypes, 10 females (with marsupium), 2 females, 2 immatures: same data as holotype; 6 males, several immature males, 8 females, 4 immatures: Parque Nacional El Avila, 10°33.01'N 66°53.88'W, high in the mountains at 1700 m (+/- 200 m), within leaf litter near cliff, leg. C. Schmidt 10.03.1998.

#### DESCRIPTION

*Colour.* Pereonites chestnut with coxal plates slightly darker, many light spots of the muscle insertions and other light areas on coxal plates and neopleurae conspicuous, umber medial line, cephalothorax chestnut with light patches.

*Cephalothorax.* Like other Venezuelan species of this genus, linea frontalis reduced, linea supra-antennal conspicuous, slightly bent above antennal sockets, compound eyes large, comprising about 26 ommatidia, vertex bearing several long tricorn-like setae (Fig. 9, Ctf).

*Pereon.* Tergites smooth and somewhat shiny, sparsely covered with tricorn-like setae, coxal plates fused without groove. Coxal plates 1–3 caudally rounded, 4–7 increasingly pointed. No noduli laterales visible in light microscope at 400x magnification (Fig. 9, Cx4).

*Pleon.* Set back from the pereon, neopleurae of pleonite 3–5 well-developed. Pleotelson pointed with latero-distal margins concave. Tip of telson tapered, bearing tricorn-like setae of various length.

*Antennula.* Three-articulate, first article strongest, with distal shield, distal article coniform, bearing at least 5 rows of aesthetascs (Fig. 9, An1).

*Antenna.* Flagellum composed of three articles, proximal article of half the length of flagellum, distal one shorter, bearing slightly longer apical organ. Peduncular articles 4 and 5 almost subequal,

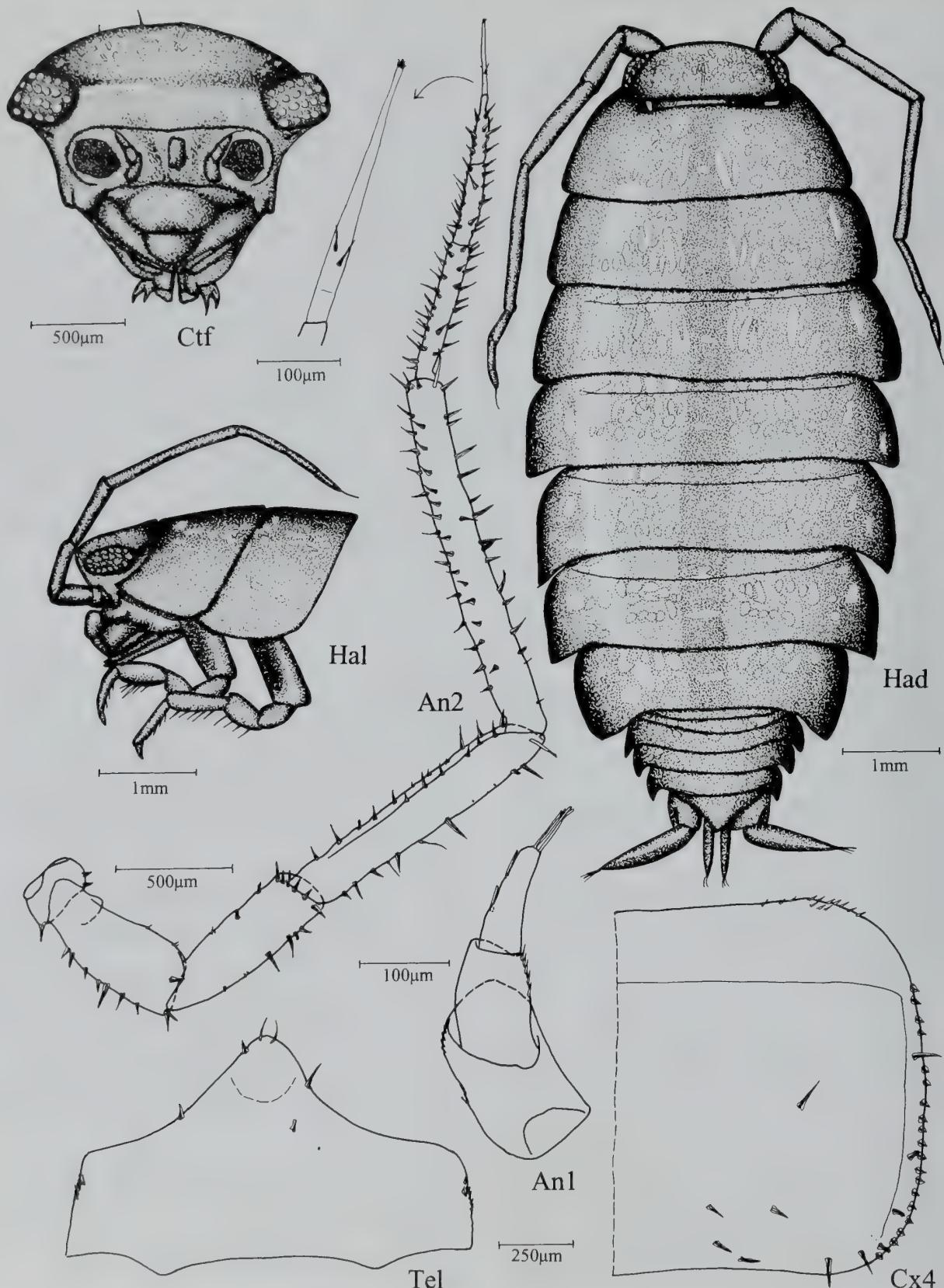


Fig. 5 *Ischiocia hirsuta* sp.nov. Holotype, male 11 mm. An1 antennula; An2 antenna with detail of apical organ; Ctf cephalothorax in frontal view; Cx4 coxal plate 4; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

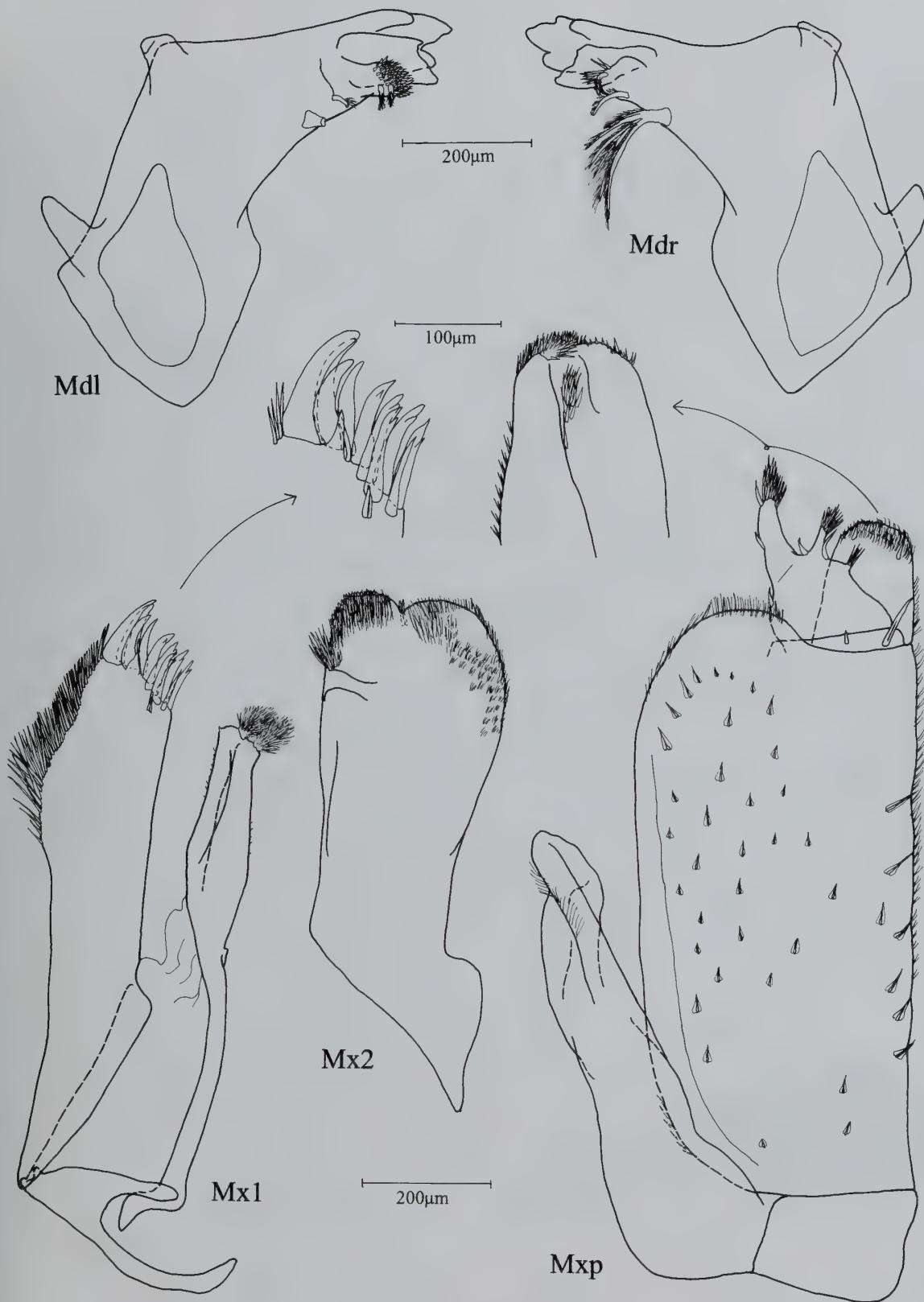
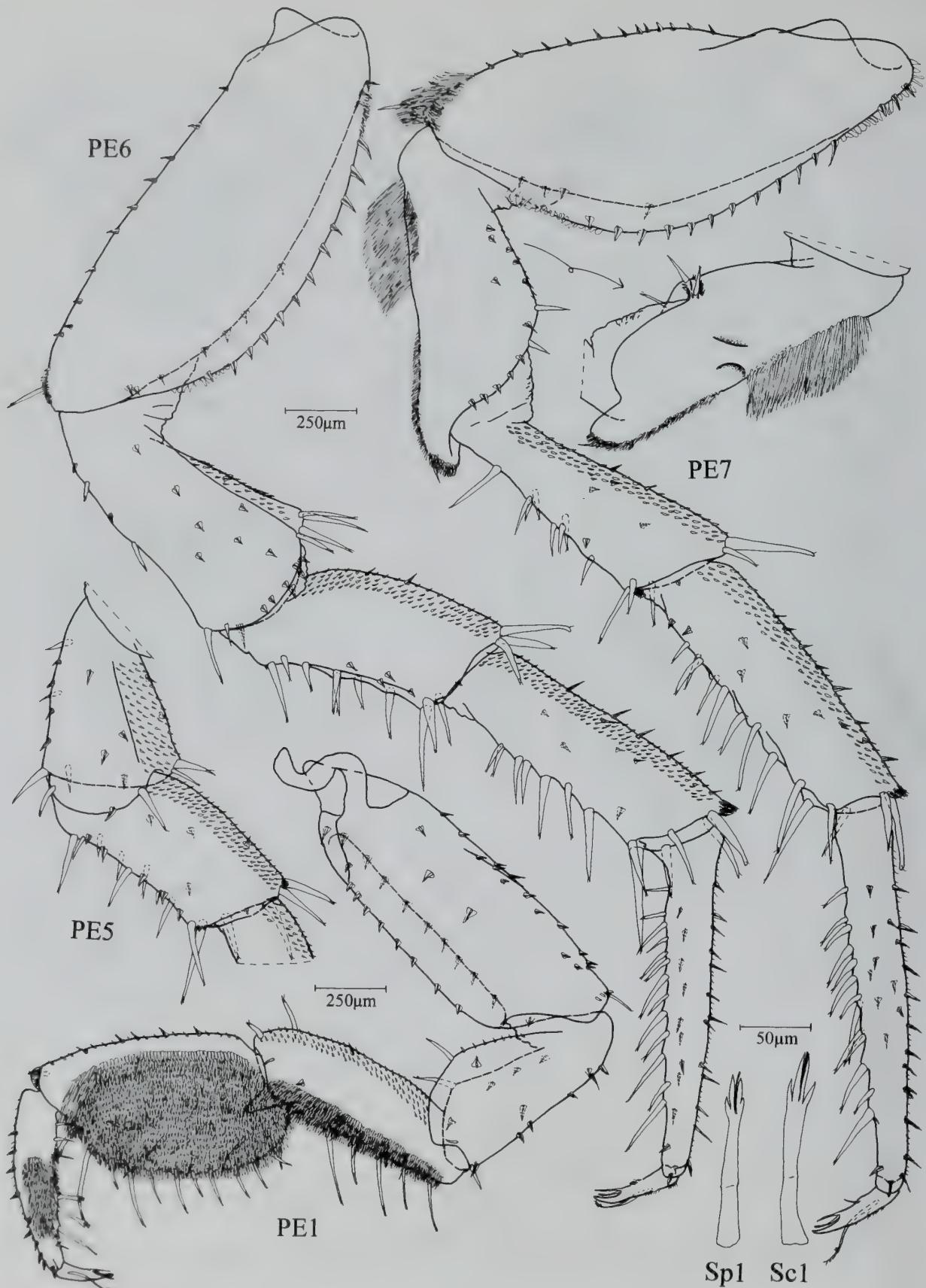
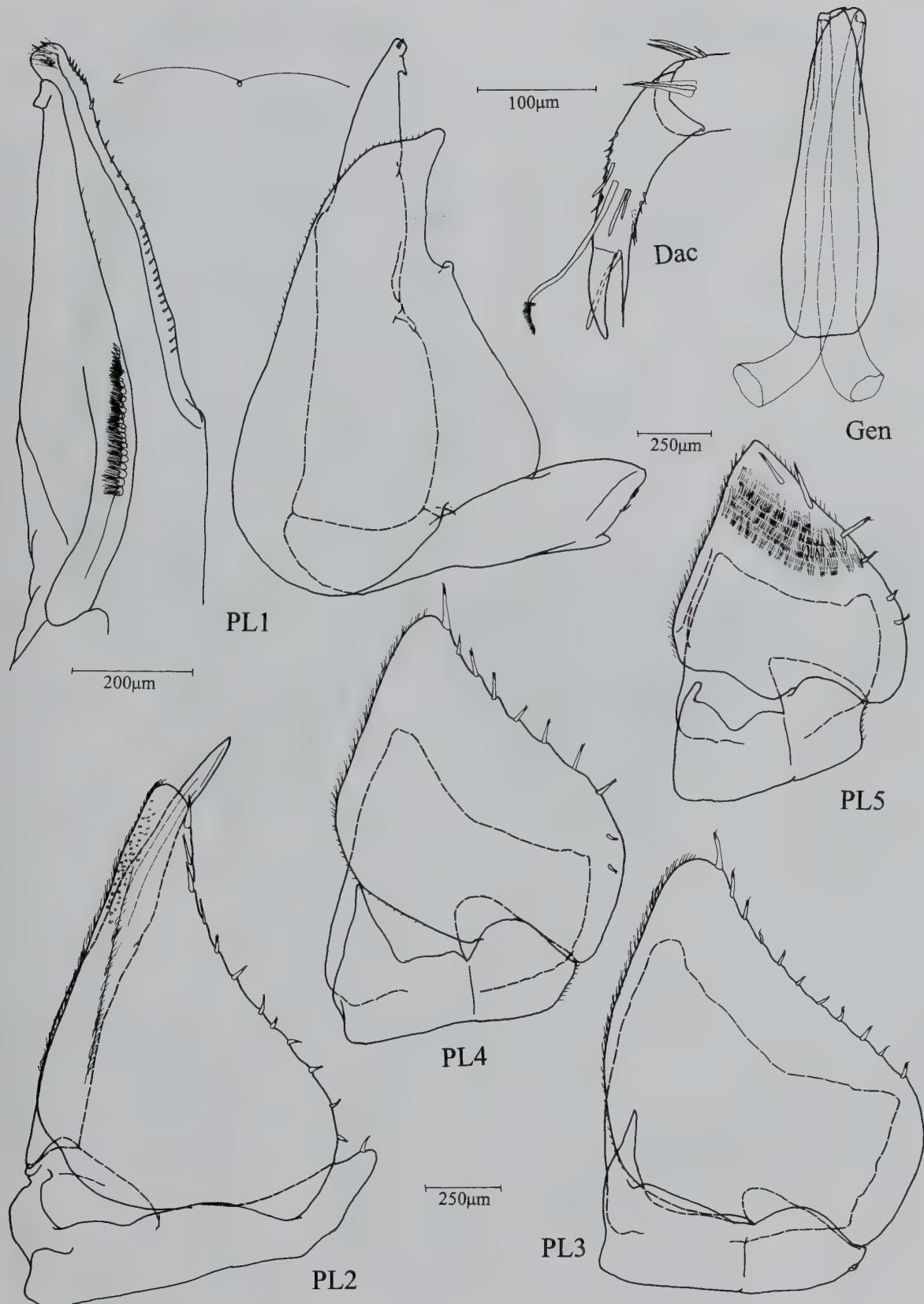


Fig. 6 *Ischioscia hirsuta* sp.nov. Holotype, male, 11 mm. Mdl/r left and right mandible; Mx1 maxillula with detail of apex of lateral endite in rostral view; Mx2 maxilla in rostral view; Mxp maxilliped, with detail of endite in rostral view.



**Fig. 7** *Ischioscia hirsuta* sp.nov. Holotype, male, 11 mm. PE1 pereopod 1 in rostral view; PE5 pereopod 5 merus and ischium in caudal view; PE6/7 pereopods 6 and 7 in caudal view, with ischium 7 in rostral view; Sc1 ornamental sensory spine of carpus 1, Sp1 distalmost sensory spine of propodus 1.



**Fig. 8** *Ischioscia hirsuta* sp.nov. Holotype, male, 11 mm. Dac dactylus 1 in rostral view; Gen genital papilla; PL1–5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

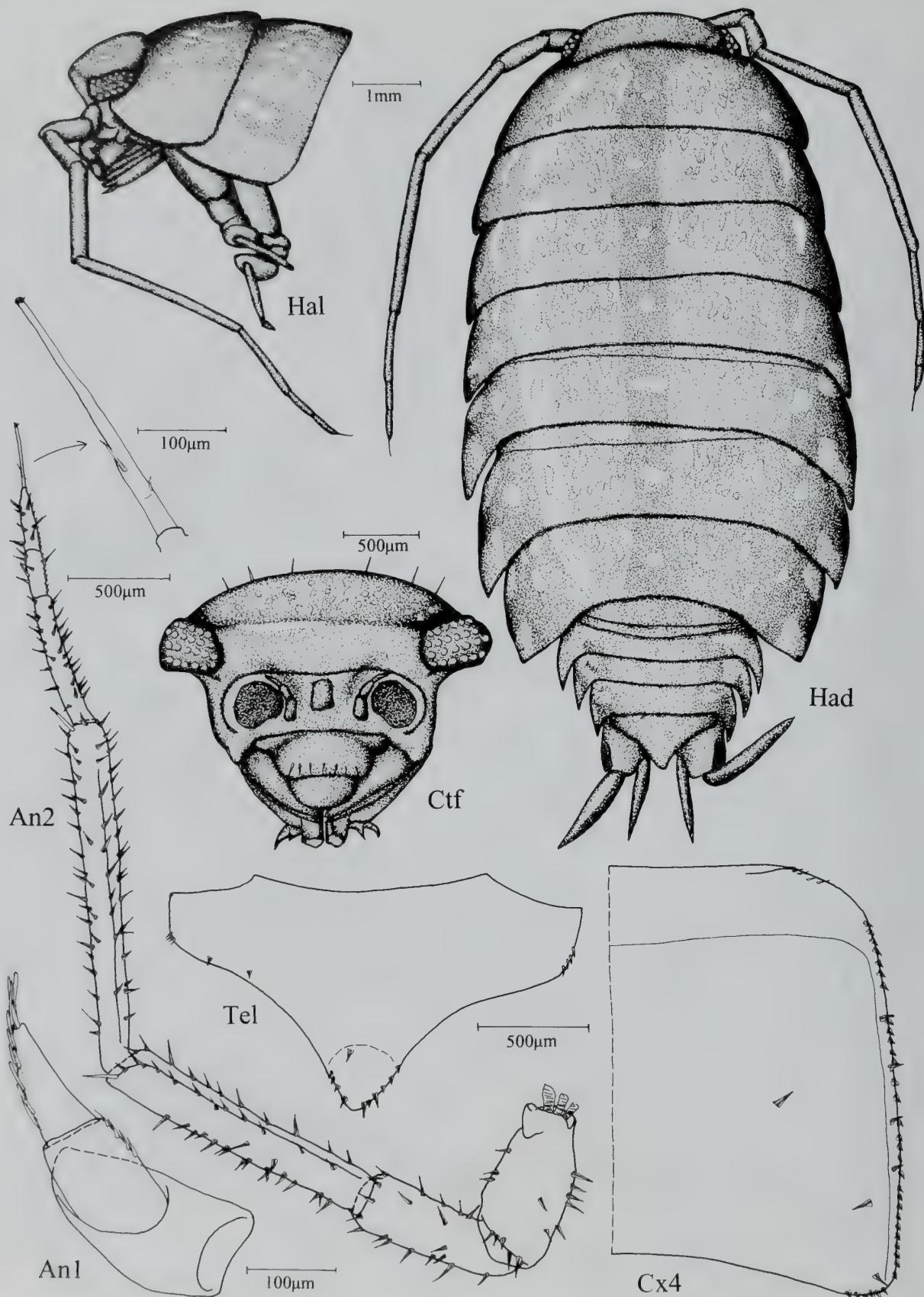
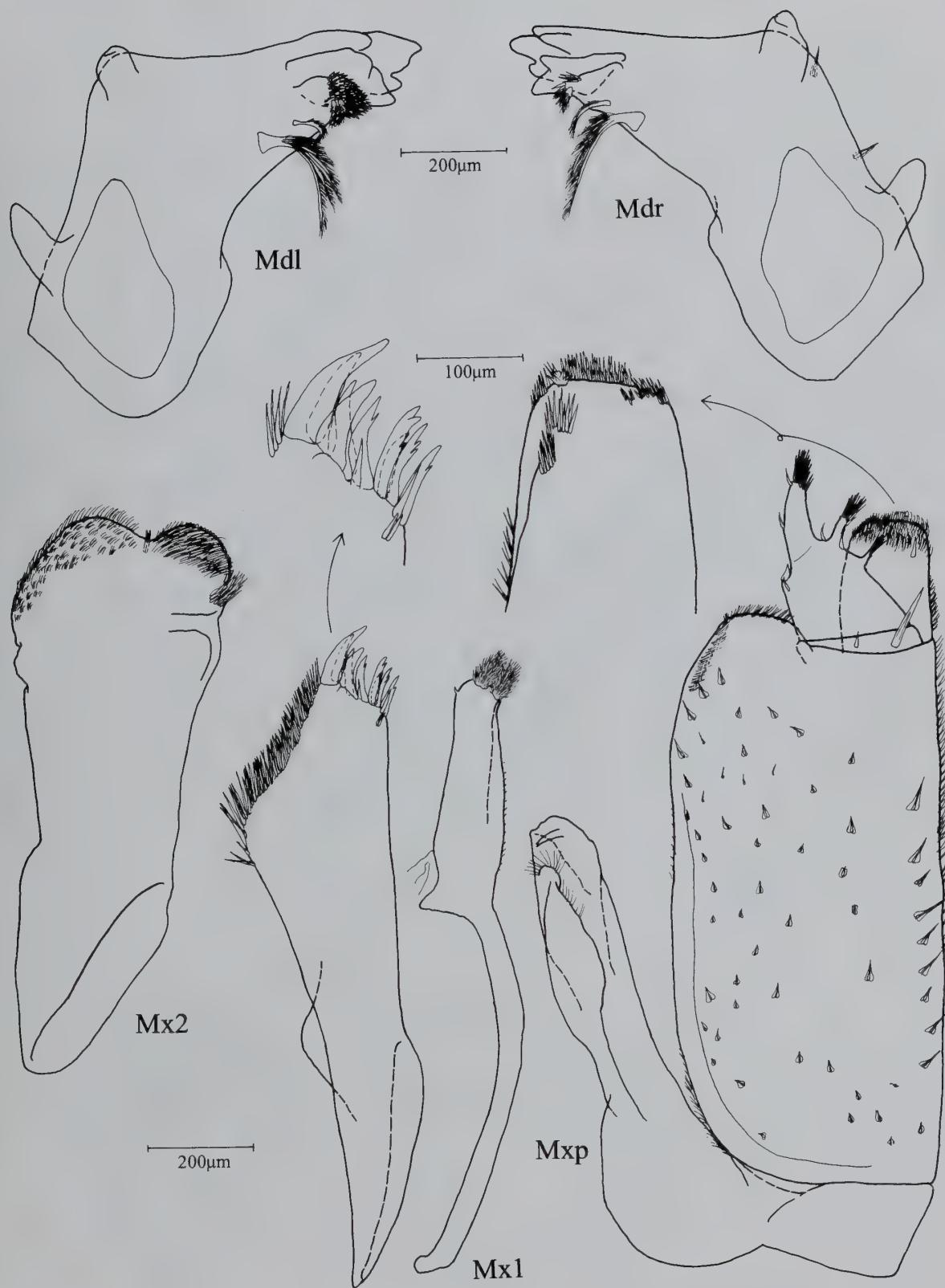


Fig. 9 *Ischioscia colorata* sp.nov. Holotype, male, 14 mm. An1 antennula; An2 antenna with detail of apical organ; Ctf cephalothorax in frontal view; Cx4 coxal plate 4; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.



**Fig. 10** *Ischioscia colorata* sp.nov. Holotype, male, 14 mm. Mdl/r left and right mandible; Mx1 maxillula with detail of apex of lateral endite in rostral view; Mx2 maxilla in rostral view; Mxp maxilliped, with detail of endite in rostral view.

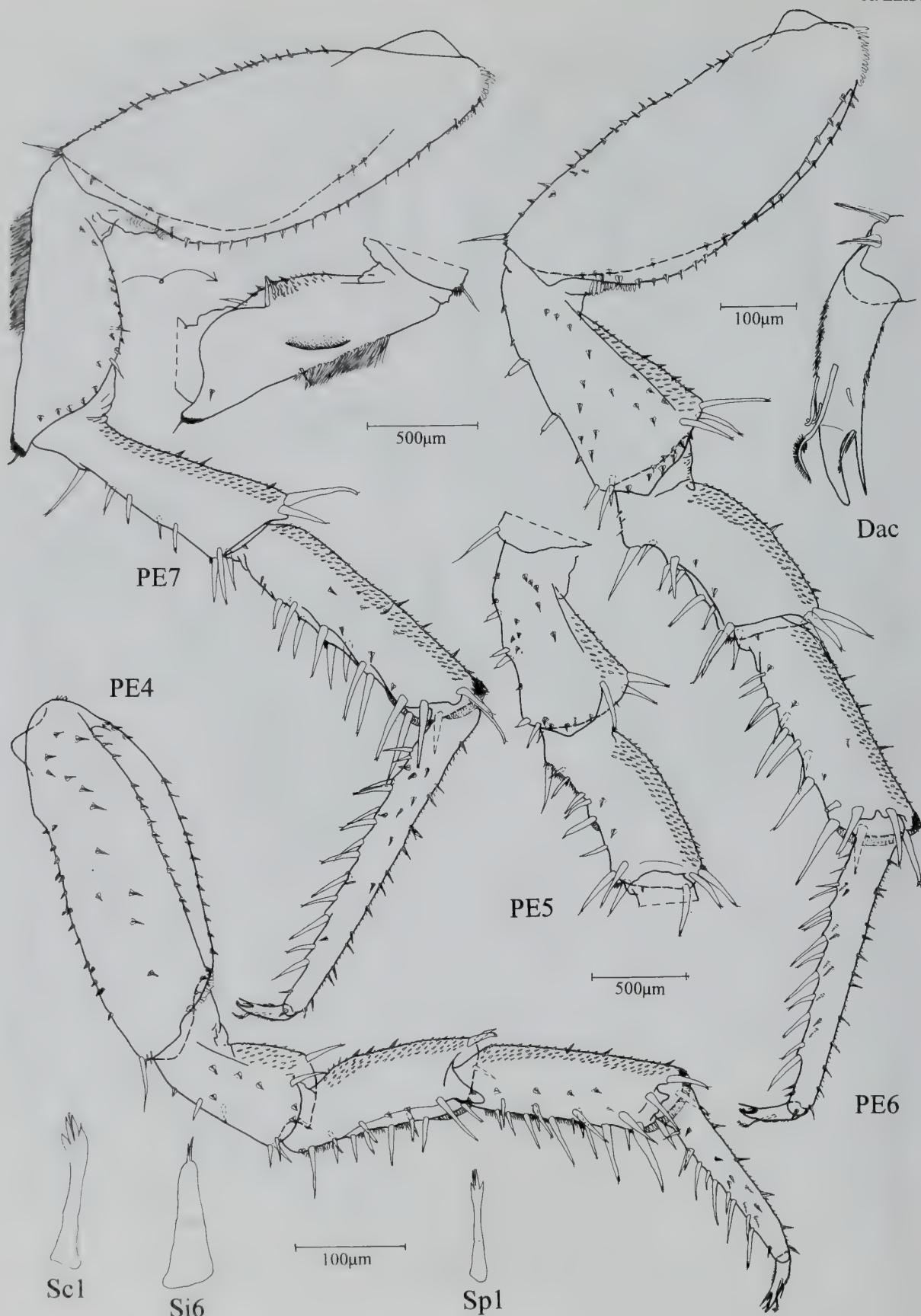
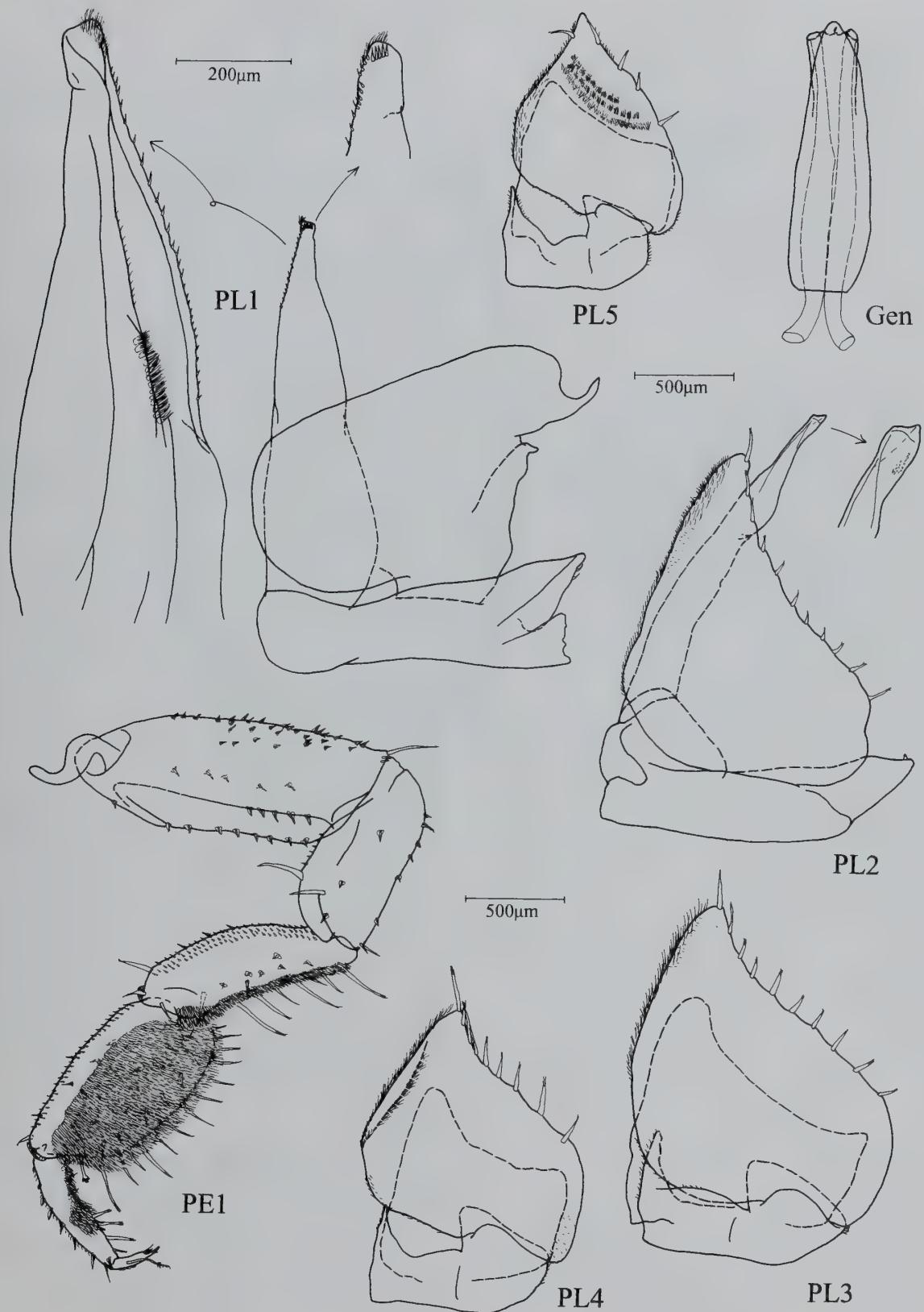


Fig. 11 *Ichiopsis colorata* sp.nov. Holotype, male, 14 mm. Dac dactylus 1 in rostral view; PE4–7 pereopods 4 to 7 in caudal view, ischium 7 in rostral view; Scl ornamental sensory spine of carpus 1; Si6 sensory spine of ischium 6; Sp1 distalmost sensory spine of propodus 1.



**Fig. 12** *Ischioscia colorata* sp.nov. Holotype, male, 14 mm. Gen genital papilla; PE1 pereopod 1 in rostral view; PL1–5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

each as long as flagellum, articles 2 and 3 half the length, proximal article short, all covered with sensory spines and tricorn-like setae (Fig. 9, An2).

**Mandible.** Molar penicil with about 7 branches, pars intermedia with coniform setae, and two penicils on left, one on right side, additional plumose seta proximally (Fig. 10, Mdl/r).

**Maxillula.** Medial endite with two stout penicils and small subapical tip, lateral endite with 4+6 teeth apically, 5 of inner set cleft, one of those double-cleft, two subapical teeth caudally, hyline lobe very slender (Fig. 10, Mx1).

**Maxilla.** Lateral endite broader than medial, covered with pectinate scales, medial lobe with denser setation, apex with about 15 cusps, setal tuft individualized (Fig. 10, Mx2).

**Maxilliped.** basipodite with sulcus lateralis and many tricorn-like setae, palp with medial and proximal setal tuft stalked, proximal more indistinctively, proximal article with long and very short seta (Fig. 10, Mxp).

**Pereopods.** Slender, as in other species of the genus (Fig. 11, PE4-7; Fig. 12, PE1), dactylus with long inner claw and apically plumose dactylar seta (Fig. 11, Dac), antenna-grooming devices on propus and carpus 1 (Fig. 12, PE1). Sexual differentiation. All pereopods sexually differentiated: pereopod 1 to 3 with enlarged carpus bearing setal fields rostrally, enlargement gradually decreasing from 1 to 3, merus and propus with setal brushes, too. Pereopod 4 with scattered setae on medial margin of carpus and merus, pereopod 5 with setal field medio-proximally on merus, ischium with four stout sensory spines medially. Pereopod 6 merus with prominent hump medio-proximally, ischium with two stout sensory spines medially, pereopod 7 merus with long proximal sensory spine and four along medial margin, ischium as in other species in the *variegata*-group, i. e. a prominent medial brush, a distal lobe and a rostral depression.

**Pleopods.** Pleopod endopodites slightly bilobate, exopodites with about 10 sensory spines laterally, medially distinctly covered with trichiae, exopodite 5 with creel of three rows of pectinate scales, distal ones parallel, proximal one diverging, protopodite 3 to 5 with slightly setose medial protrusion, laterally no rudimental epipodites, only few trichiae (Fig. 12, PL1-5). Sexual differentiation. Male pleopod 1 exopodite obtuse triangular, lateral point recurved, incision with transverse folding proximally on caudal side, endopodite straight, apex obtuse, rostrally with 5 to 6 teeth, caudally with tuft of hyaline trichiae, lateral row of spines present. Pleopod 2 exopodite elongate with sinuous lateral margin bearing 11 sensory spines, medially with trichiae, endopodite with truncate apex, bearing some faint granules caudally.

**Uropod.** Exopodite and endopodite subequal in length.

**Genital papilla.** Ventral shield slightly surpassing terminal spatula (Fig. 12, Gen).

**ETYMOLOGY.** The specific name refers to the colourful dorsal tegument.

### *Ischioscia pariae* sp.nov.

Figs 13-16

**MATERIAL EXAMINED.** Holotype, male (body length 10 mm): Península de Paria, El Refugio de la Cerbatana, primary forest with high trees covered with Bryophyta, Bromeliaceae, Lycopodiaceae, vines, very humid, in leaf litter, leg. C. Schmidt 04.04.1998. Paratypes: 4 males, 6 females, 7 immatures: same data as holotype; 7 males, 7 females (with marsupium), 8 females: Península de Paria, El Rincón, 10°35'59.4" N 63°11'8.1" W, small brook, water only in upper half, humid forest, lower part in coacoa

plantation, with some very high Bombacaceae, near small well, leg. C. Schmidt 09.04.1998.

### DESCRIPTION

**Colour.** Basic colour chestnut, prominent light patches on medial line of tergites and coxal plates, between them smaller irregular patches, caudal patches on median line dark umber, pleon chestnut with white patches in medial line, cephalothorax covered with small white spots, representing muscle insertions.

**Cephalothorax.** Linea supra-antennalis prominent, linea frontalis lacking, with lamina frontalis, vertex flat, covered with some setae, compound eyes consisting of 25 ommatidia in 4 rows (Fig. 13, Ctf).

**Pereon.** Tegument rather smooth and shiny, coxal plates 1 to 3 rounded, coxal plates 4 to 7 caudally pointed, no noduli laterales nor gland pores discernible, sulcus marginalis present.

**Pleon.** Retracted from pereon, pleonites 3 to 5 with small neopleurae, pleotelson with concave margins, densely covered with small cuticle-covered sensilla.

**Antennula.** As in other species of genus, differing in position of aesthetascs on distal article, which are inserted at almost entire medial margin (Fig. 13, An1).

**Antenna.** Peduncle rather long with typical length ratio of other members of the genus, flagellum with proximal article longest, of half length of flagellum, apical organ longer than medial article (Fig. 13, An2).

**Mandible.** Molar penicil composed of about 7 branches, additional plumose seta long, pars intermedia with two penicils on left and one on right mandible, coniform setae on both sides (fig. 14, Mdl/r).

**Maxillula.** Medial endite with two stout penicils and small subapical tip, lateral endite bearing 4+6 teeth apically, five of inner set cleft, on caudal side with hyaline lobe, stalk and two slender subapical teeth, laterally fringed with trichiae (Fig. 14, Mx1).

**Maxilla.** Lateral lobe slightly broader than medial one, covered with pectinate scales and faint trichiae, medial lobe densely covered with trichiae, apically with about 15 cusps (Fig. 14, Mx2).

**Maxilliped.** Basipodite with sulcus lateralis, palp with one seta on proximal article, medial article with two setal tufts, distal one stalked, distal article with prominent setal tuft, endite caudally setose with two teeth, rostrally with prominent penicil (Fig. 14, Mxp).

**Pereopods.** Pereopod 1 carpus and propus with antenna-grooming brushes (Fig. 15, PE2-7; Fig. 16, PE1), dactylus with a hyaline cuticular scale laterally of main claw, inner claw long, dactylar seta with an enlarged apex, subapically some plumules (Fig. 15, Dac). Sexual differentiation. Male pereopods 1 to 3 with enlarged carpus and prominent setal fields rostrally, carpus 2 and 3 only slightly enlarged, merus 1 to 3 with medial setal field, setal field present on propus 2, too. Pereopod 7 ischium with distal lobe, sparsely covered with trichiae, setal brush on medio-proximal half slightly directed rostrodistally, more laterally accompanied by a prominent groove extending to the lateral margin, two sensory spines on lateral margin.

**Pleopods.** Endopodites more rectangular and exopodites more triangular as in preceding species, especially in pleopod 5, laterally bearing 6 to 8 sensory spines, protopodite 3 to 5 lacking rudimental epipodites (Fig. 16, PL1-5). Sexual differentiation. Pleopod exopodite triangular with rounded medial edge and slightly sinuous medial margin, almost continued by lateral protrusion, incision proximally bordered by a step-like additional tip, endopodite straight, apically pointed with small lateral protrusion subapically, caudolateral row of minute spines, single prominent spine apically. Pleopod 2 with only slightly sinuous lateral margin bearing 8 sensory spines, endopodite with apex shaped like a hypodermal needle.

**Uropod.** Exopodites rather long (Fig. 13, UR).

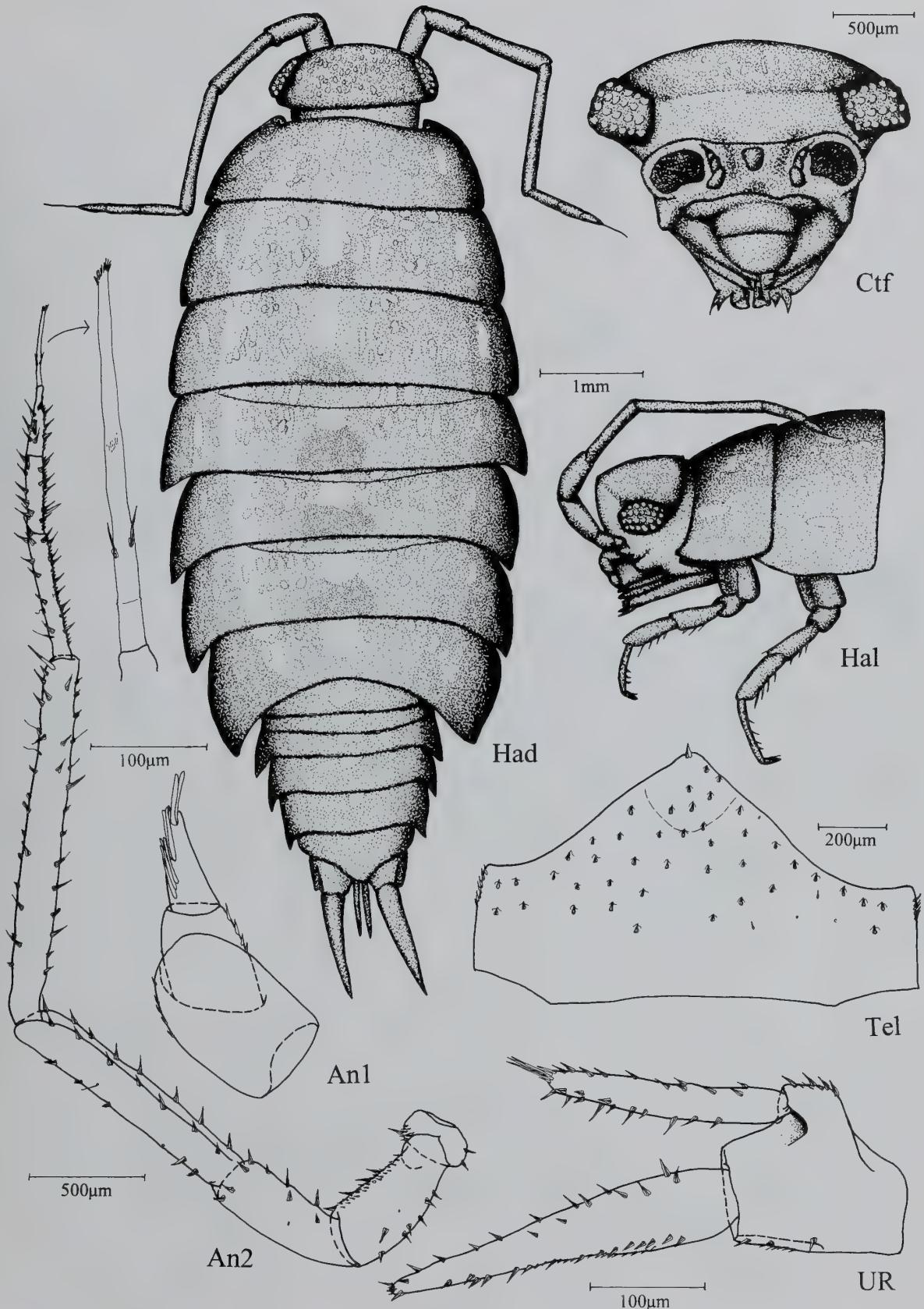
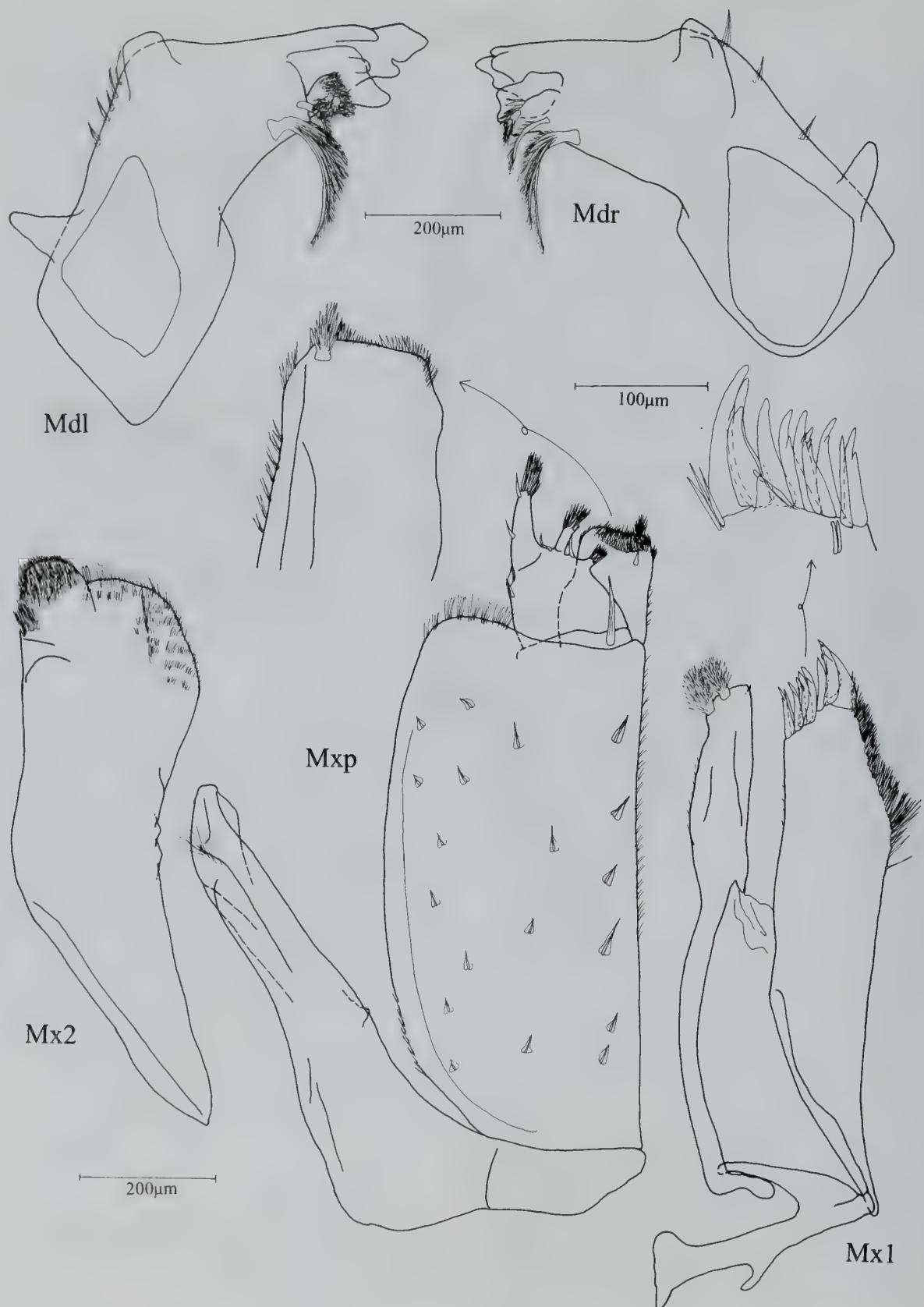
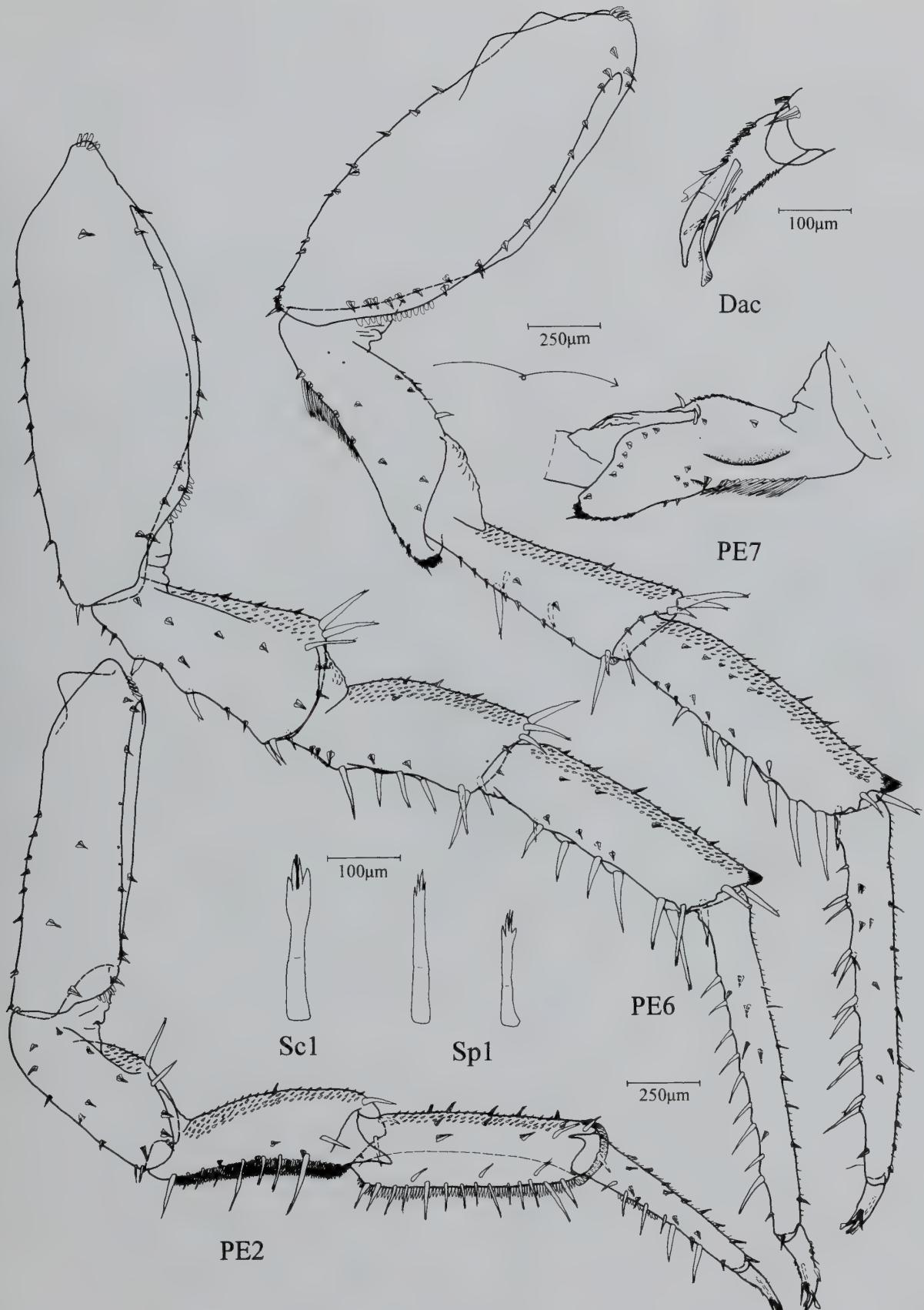


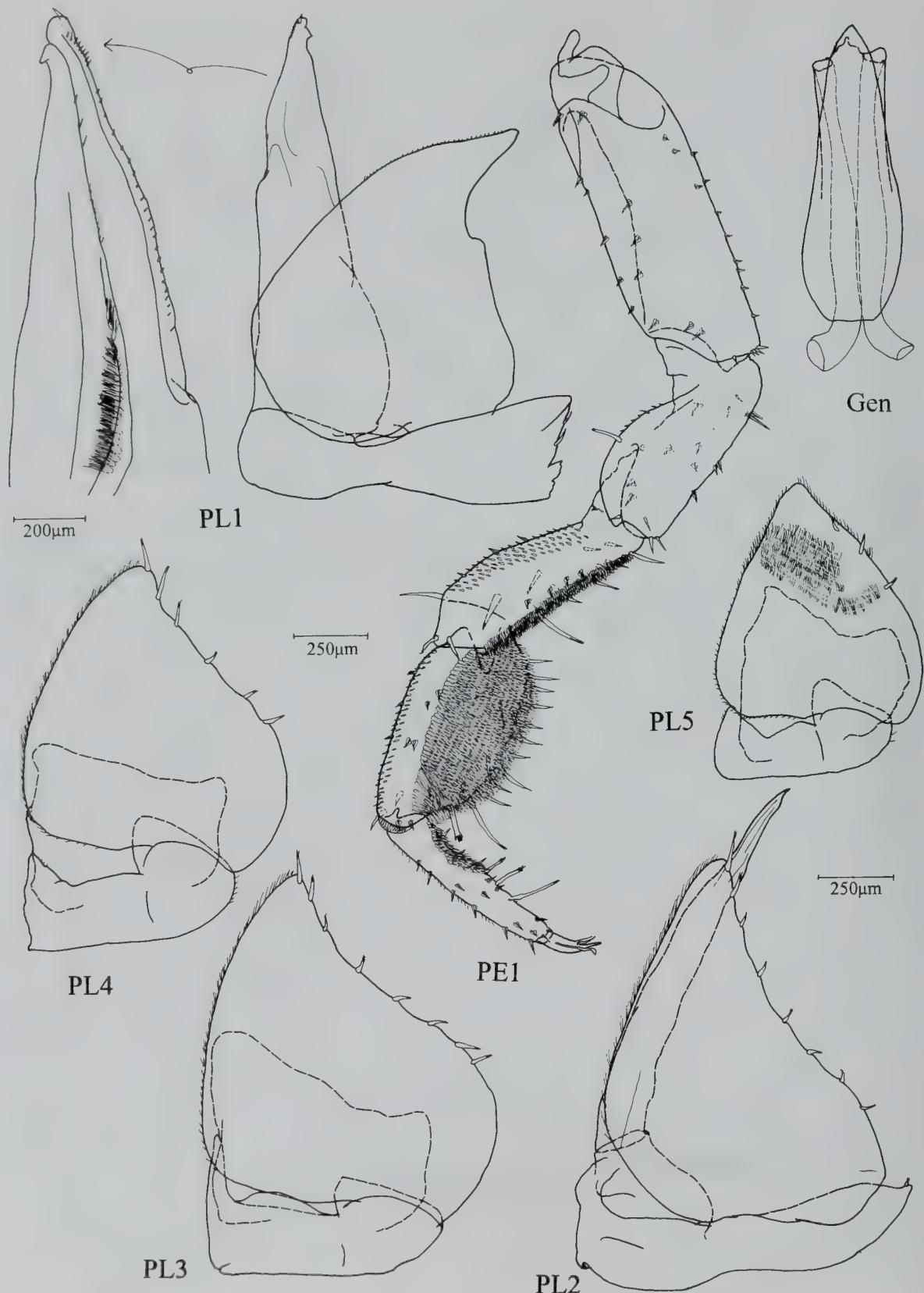
Fig. 13 *Ischioscia pariae* sp.nov. Holotype, 13 mm. An1 antenna; An2 antenna with detail of apical organ; Ctf cephalothorax in frontal view; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson; UR uropod in rostral view.



**Fig. 14** *Ichioscia pariae* sp.nov. Holotype, 13 mm. Mdl/r left and right mandible; Mx1 maxillula in caudal view, with detail of apex of lateral endite in rostral view; Mx2 maxilla in rostral view; Mxp maxilliped, with detail of endite in rostral view.



**Fig. 15** *Ischioscia pariae* sp.nov. Holotype, 13 mm. Dac dactylus 1 in rostral view; PE2–7 pereopods 2, 6, 7 in caudal view, ischium 7 in rostral view; Sc1 ornamental sensory spine and proximal sensory spine of carpus 1; Sp1 distalmost sensory spine of propodus 1.



**Fig. 16** *Ischioscia pariae* sp.nov. Holotype, 13 mm. Gen genital papilla; PE1 pereopod 1 in rostral view; PL1–5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

*Genital papilla.* Ventral shield distinctly surpassing terminal spatula (Fig. 16, Gen).

ECOLOGICAL NOTE. This species is capable of jumping about 5 cm.

ETYMOLOGY. The species name refers to the distribution on Península de Paria.

### *Ischioscia guamae* sp.nov.

Figs 17–20

MATERIAL EXAMINED. Holotype, male (body length 13 mm): Rio La Guama, 9°46.48' N 68°24.6' W, river valley between dry mountains, in leaf litter, leg. C. Schmidt 25.03.1998. Paratypes 1 males, 3 females 11 immatures: same data as holotype.

#### DESCRIPTION

*Colour.* Ground colour chestnut with several light markings on cephalothorax and pereonites, coxal plates with light margins, in coxal plates V to VII, two light patches instead of contiguous band, dark chestnut spot in the mid line of pereonite I to IV caudally, pleon bearing several pale spots.

*Cephalothorax.* Linea frontalis lacking, lamina frontalis and linea supra-antennalis prominent. Vertex smooth and free of setation, laterally protruding compound eyes composed of 22 ommatidia in four rows (Fig. 17, Ctf).

*Pereon.* Tegument smooth and shiny, bearing scattered setae, coxal plates 1 to 4 caudally rounded, coxal plates 5 to 7 increasingly pointed, sulcus marginalis present, no gland pores nor noduli laterales discernible in light microscope at 400x magnification (Fig. 17, Cx3).

*Pleon.* Set back from pereon despite neopleurae of pleonite 3 to 5. Pleotelson rather pointed, lateral margins concave, some tricorn-like setae apically.

*Antennula.* Similar to other species of genus (Fig. 17, An1).

*Antenna.* Rather short, flagellum three-articulate, with proximal article longest, somewhat shorter than peduncular article 5, tricorn-like setae on all articles, apical organ half as long as flagellum (Fig. 17, An2).

*Mandible.* Pars intermedia with two penicils on left and one on right side, several coniform setae, molar penicil composed of about 7 branches, additional plumose seta prominent (Fig. 18, Mdl/r).

*Maxillula.* Medial endite with two stout penicils and very small subapical tip, lateral endite apically with 4+6 teeth, 4 of inner set cleft, 2 very slender, caudally with hyaline lobe and slender subapical tooth (Fig. 18, Mx1).

*Maxilla.* Lateral lobe broader than medial lobe, covered with faint trichiae and pectinate scales, medial lobe densely setose, apically with about 15 cusps (Fig. 18, Mx2).

*Maxilliped.* Palp with three setal tufts medially, distal two very prominent, proximal article bearing long and short seta, endite with knob-like penicil on rostral side, caudally setose with two teeth, basipodite with sulcus lateralis (Fig. 18, Mxp).

*Pereopods.* Slender (Fig. 19, PE1–7), with dactylus bearing plumose dactylar seta and long inner claw (Fig. 19, Dac), pereopod 1 carpus with antenna-grooming brush and ornamental sensory spine with hand-like apex (Fig. 19, Sc1), propus 2 with antenna-grooming comb.

Sexual differentiation. Pereopod 1 to 3 and 7 differentiated, propus 1 and 2, carpus and merus 1 to 3 with setal brush, carpus medially enlarged, conspicuously in pereopods 1 to 2, slightly in pereopod 3. Pereopod 7 ischium with setose medio-distal lobe, setal brush subproximally to half length, no rostral depression, merus 7 of characteristic shape, 2 medio-caudal sensory spines on proximal half.

*Pleopods.* Similar to other species of the genus, exopodites laterally with sensory spines, medially with minute pectinate scales, no

rudimental epipodites on protopodites 3 to 5 (Fig. 20, PL1–5). Sexual differentiation. Male pleopod 1 exopodite triangular with lateral incision bordered by lateral point and proximal protrusion, endopodite with wrinkled apex and subapical lateral protrusion, caudal row of spines reduced, some spines on apex, two of them very prominent, surpassing apex. Pleopod 2 endopodite slightly sinuous laterally, bearing about 7 sensory spines, endopodite slightly surpassing exopodite, apex pointed.

*Uropod.* As in other species of the genus.

*Genital papilla.* Ventral shield slightly surpassing terminal spatula (Fig. 20, Gen).

ETYMOLOGY. The species name is derived from Rio La Guama, the type locality.

### *Ischioscia trifasciata* sp.nov.

Figs 21–24

MATERIAL EXAMINED. Holotype, male (body length 13 mm), Rancho Grande, 10°21'N 67°41'W, in ground traps 30 cm diameter, leg. O. Hernández 1995. Paratypes: several males and females: same data as holotype.

#### DESCRIPTION

*Colour.* Dorsal tegument rich chestnut with many yellowish patches, medial line and coxal plates dark umber brown, forming three bands, margin of coxal plates lighter, pleon chestnut with pairs of light spots on each pleonite, cephalothorax chestnut, vertex heavily spotted yellowish.

*Cephalothorax.* As in other species of *Ischioscia* with large, laterally protruding compound eyes composed of about 24 ommatidia, vertex somewhat flattened, linea frontalis lacking, linea supra-antennalis conspicuous, only slightly sinuous, between antennal sockets with prominent lamina frontalis (Fig. 21, Ctf).

*Pereon.* Coxal plates of pereonite 1–3 with rounded margins, fourth to seventh coxal plate increasingly caudally pointed, no noduli laterales. Tegument smooth with only few tricorn-like setae (Fig. 21, Cx4).

*Pleon.* Retracted from pereon, pleonites 3–5 with small neopleurae. Pleotelson with concave latero-distal margins, as long as protopodites of uropods, tricorn-like setae gathered at apex.

*Antennula.* Apex of three-articulate antennula coniform, terminated by tuft of three aesthetascs, row of at least four aesthetascs on medial border. Some hairlike setae on median article (Fig. 21, An1).

*Antenna.* Peduncular articles with various sensory and tricorn-like setae as dense as on flagellum. Fifth article the longest, fourth 3/4 the length of fifth, as long as third and second together, those subequal. Flagellar articles subsequently shorter, together longer than fourth peduncular article, apical organ of same length as distal flagellar article (Fig. 21, An2).

*Mandible.* Pars intermedia with two stout penicils on left, one on right mandible, proximally additional penicil, molar penicil composed of 6 to 7 branches (Fig. 22, Mdl/r).

*Maxillula.* Medial endite with 2 stout penicils apically, small apical tip, lateral endite laterally fringed with trichiae, apically bearing 4+6 teeth, 5 of inner set cleft, caudally with hyaline lobe, stalk and two small teeth with fringed apex (Fig. 22, Mx1).

*Maxilla.* Both lobes subequal in breadth, densely covered with faint trichiae, medial lobe apically with about 12 cusps (Fig. 22, Mx2).

*Maxilliped.* Basipodite with sulcus lateralis, endite with tooth and dense setation caudally, rostrally with conspicuous knob-like penicil, palp with proximal article bearing two unequal setae, distal articles fused without a groove, three setal tufts of 7 to about 25 setae, proximal and medial stalked (Fig. 22, Mxp).

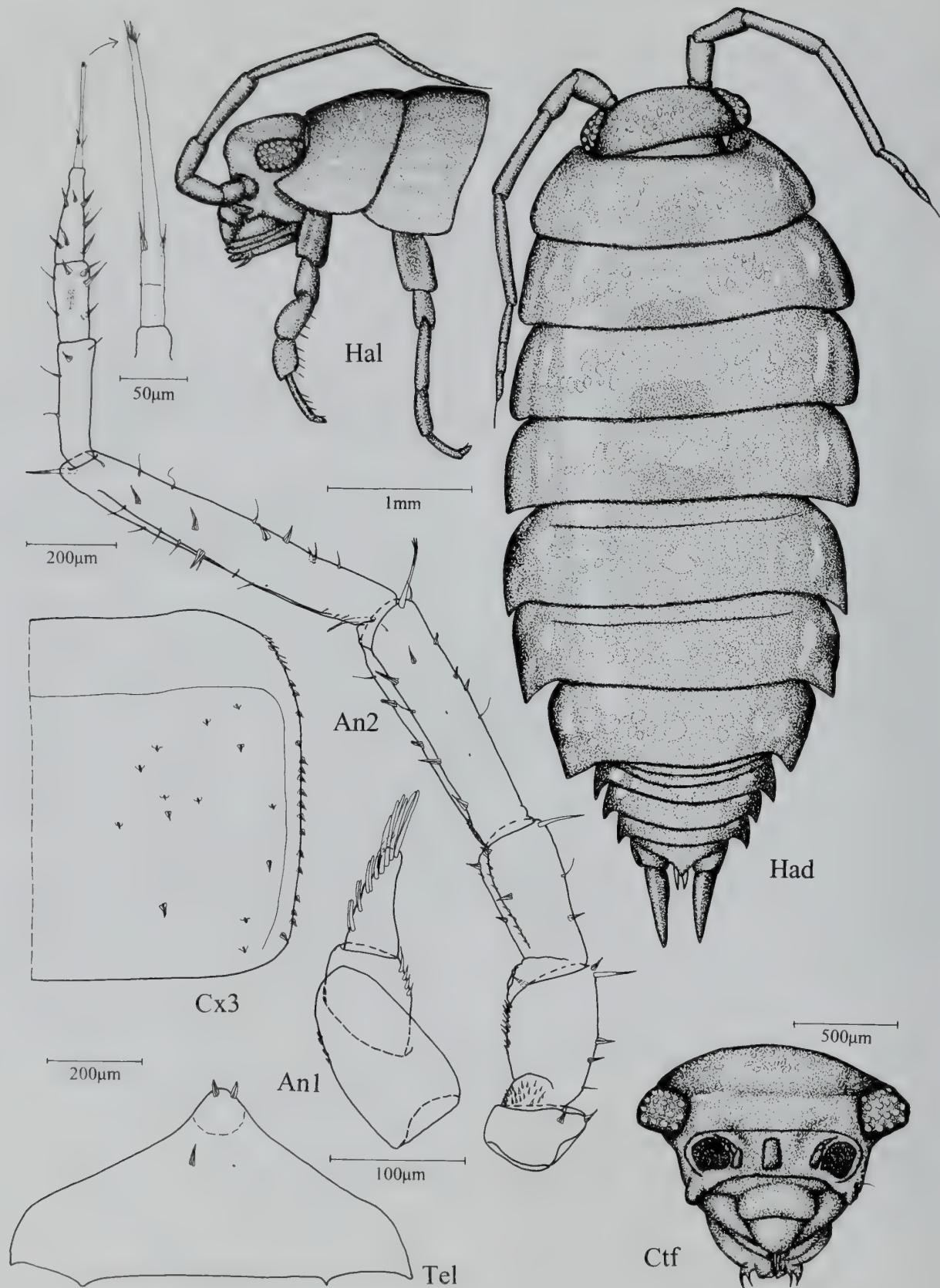
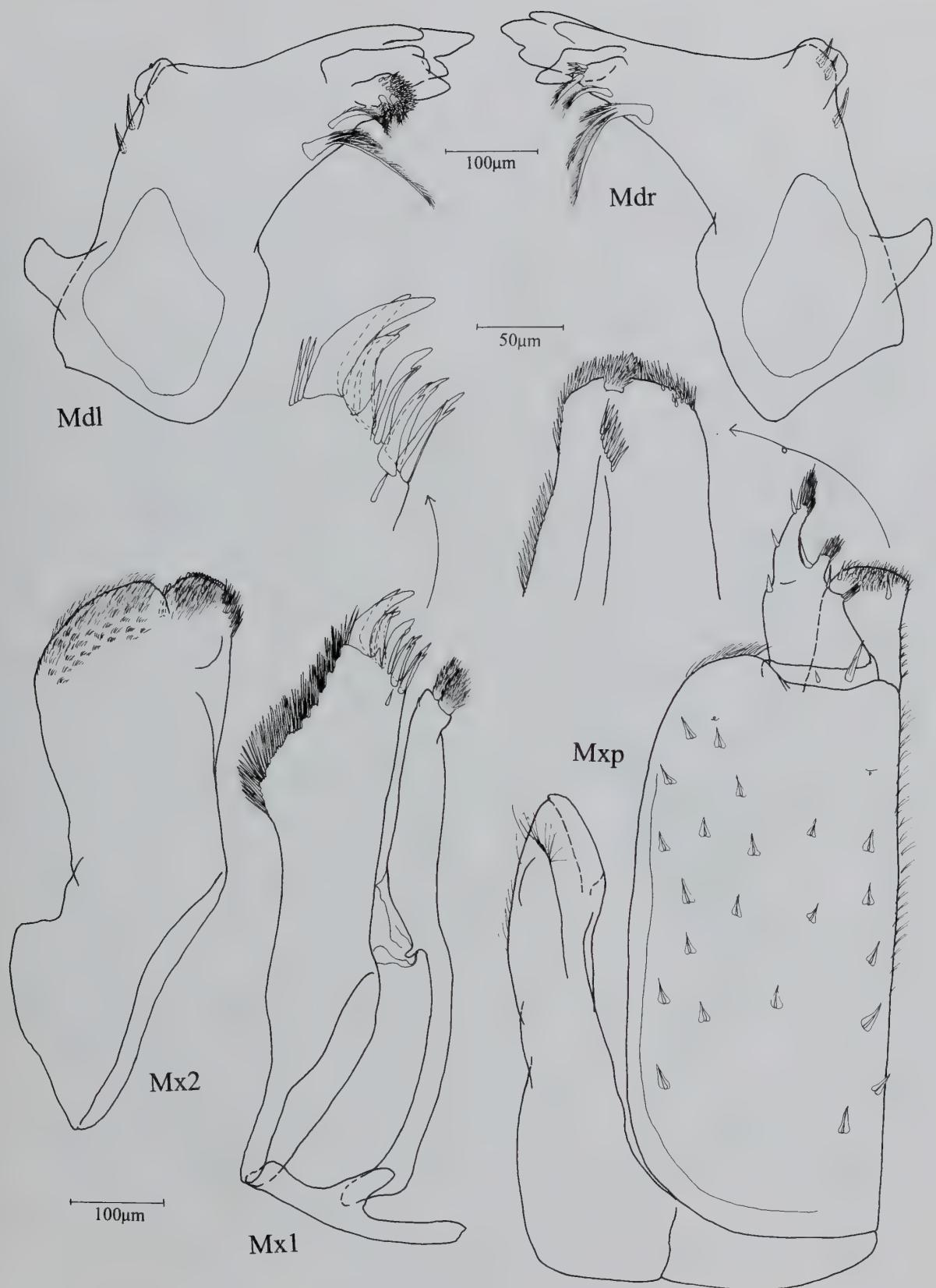
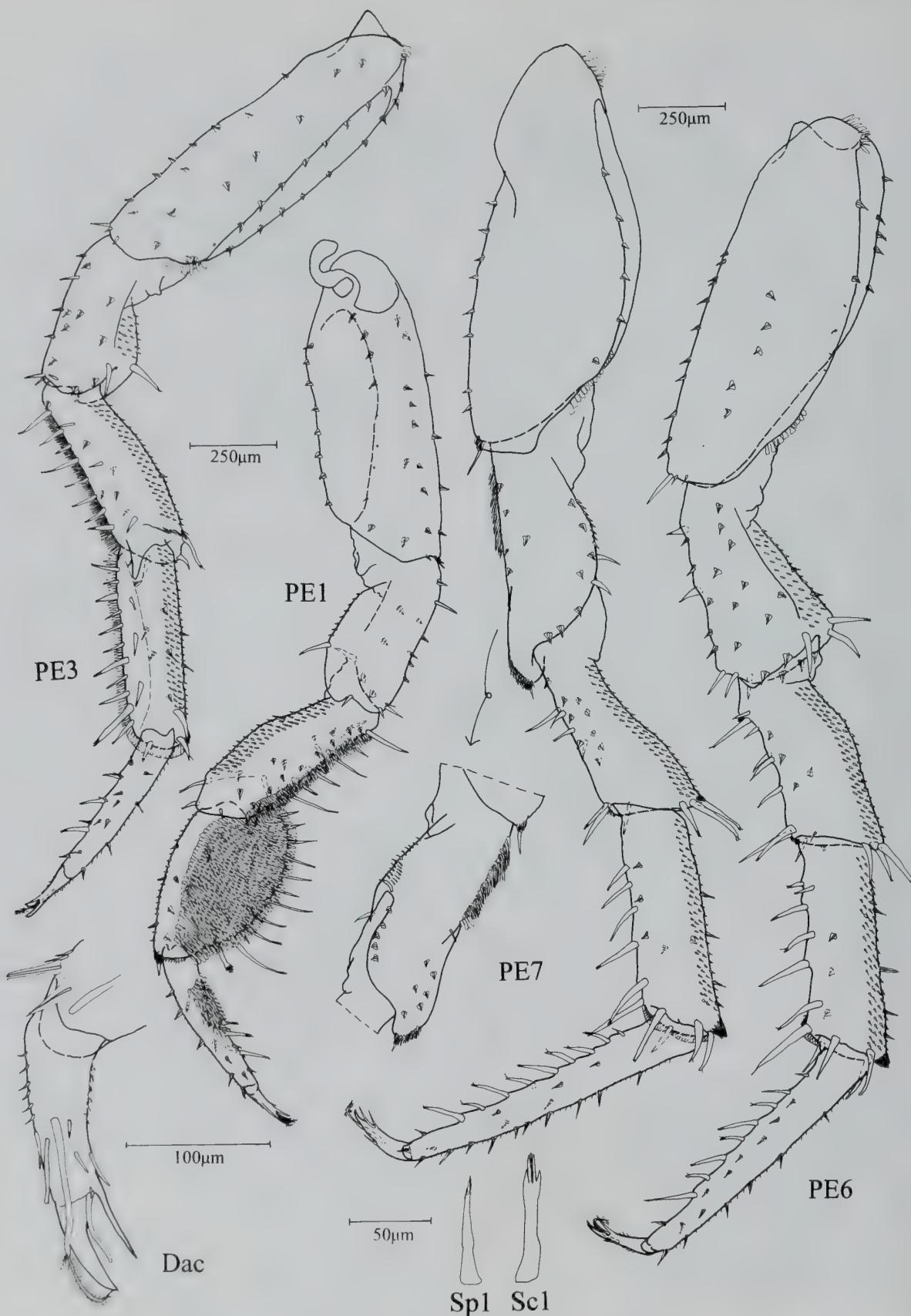


Fig. 17 *Ichiostcia guamae* sp.nov. Holotype, male 13 mm. An1 antennula; An2 antenna with detail of apical organ; Ctf cephalothorax in frontal view; Cx3 coxal plate 3; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.



**Fig. 18** *Ischioscia guamae* sp.nov. Holotype, male 13 mm. Mdl/r left and right mandible; Mx1 maxillula with detail of apex of lateral endite in rostral view; Mx2 maxilla in rostral view; Mxp maxilliped, with detail of endite in rostral view.



**Fig. 19** *Ichioscia guamae* sp.nov. Holotype, male 13 mm. Dac dactylus 1 in rostral view; PE1 pereopod 1 in rostral view; PE3–7 pereopods 3, 6, 7 in caudal view, ischium 7 in rostral view; Sc1 ornamental sensory spine of carpus 1; Sp1 distalmost sensory spine of propus 1.

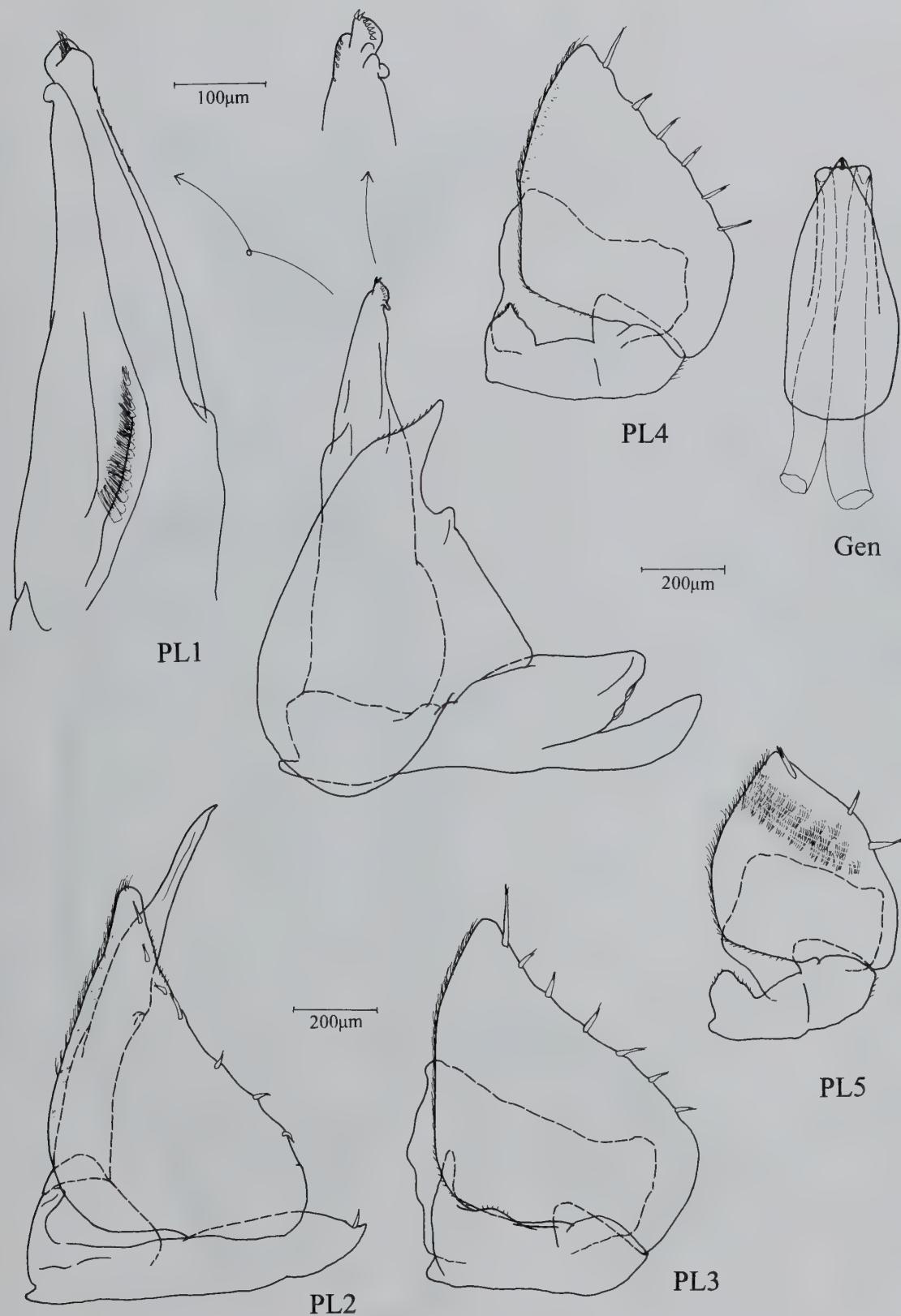


Fig. 20 *Ischioscia guamae* sp.nov. Holotype, male 13 mm. Gen genital papilla; PL1–5 pleopods 1 to 5, rostral view, with detail of endopodite 1 in rostral and caudal view.

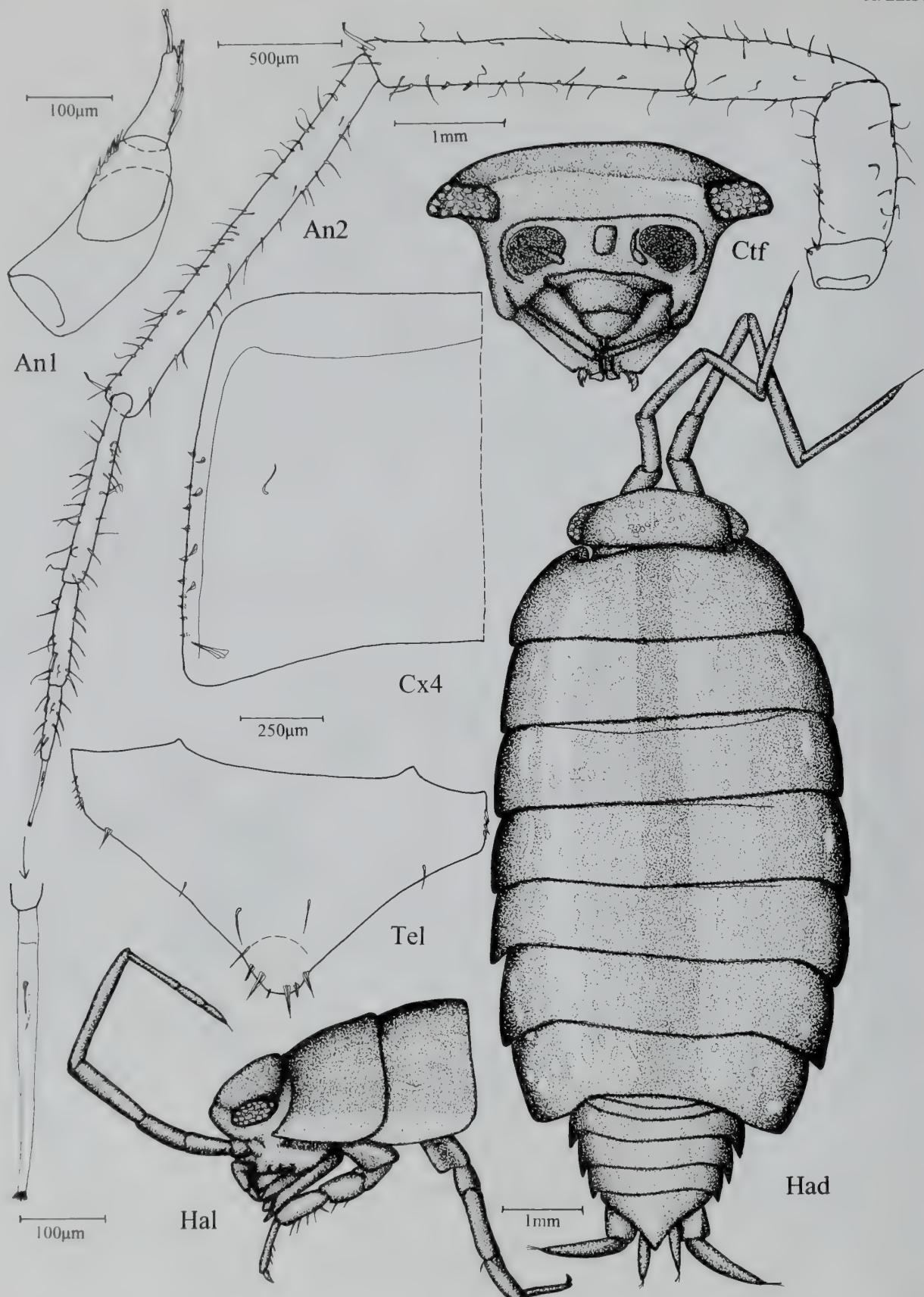


Fig. 21 *Ischioscia trifasciata* sp.nov. Holotype, male 13 mm. An1 antennula; An2 antenna with detail of apical organ; Ctf cephalothorax in frontal view; Cx4 coxal plate 4; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

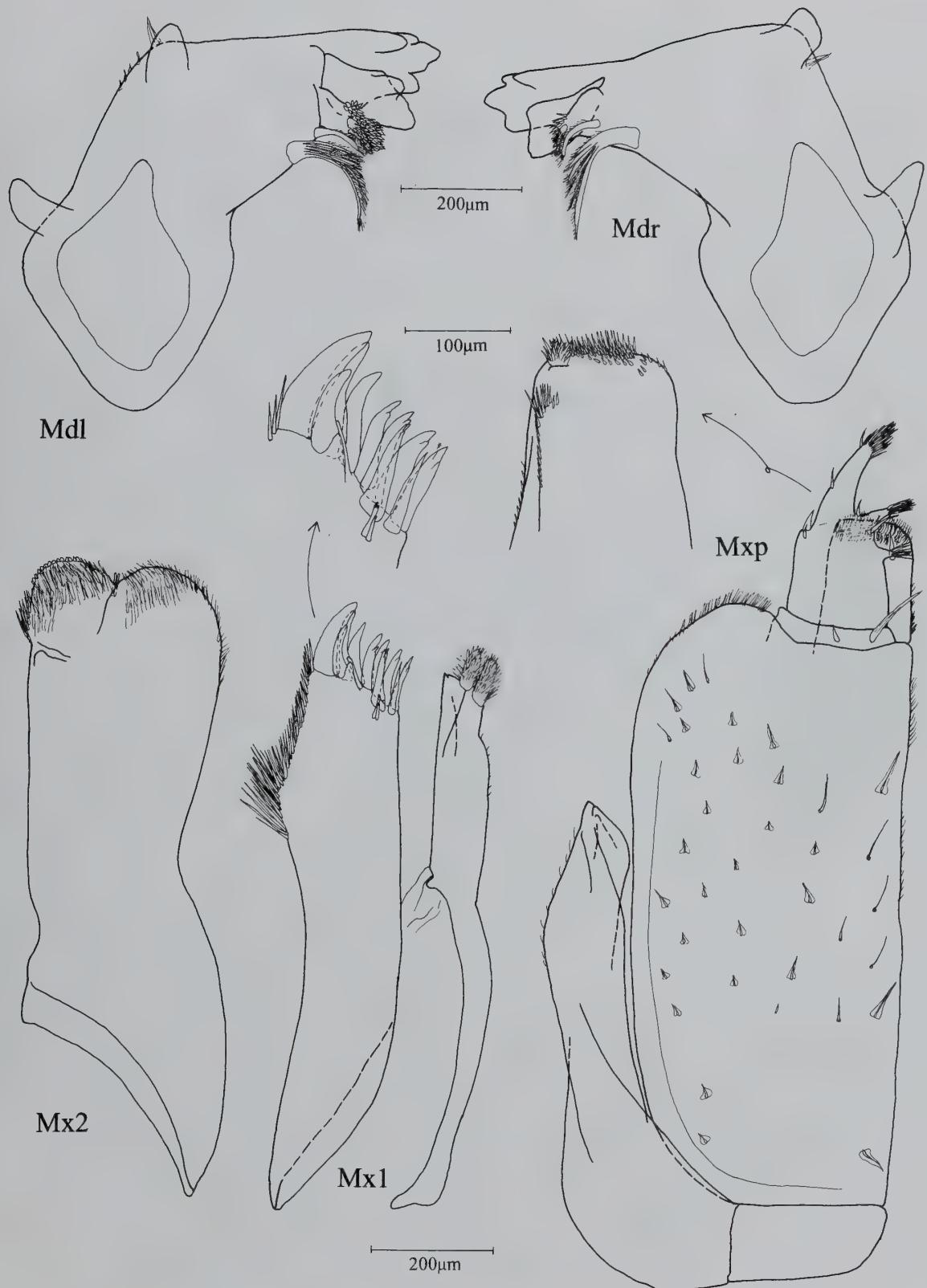


Fig. 22 *Ischioscia trifasciata* sp.nov. Holotype, male 13 mm. Mdl/r left and right mandible; Mx1 maxillula with detail of apex of lateral endite in rostral view; Mx2 maxilla in rostral view; Mxp maxilliped, with detail of endite in rostral view.

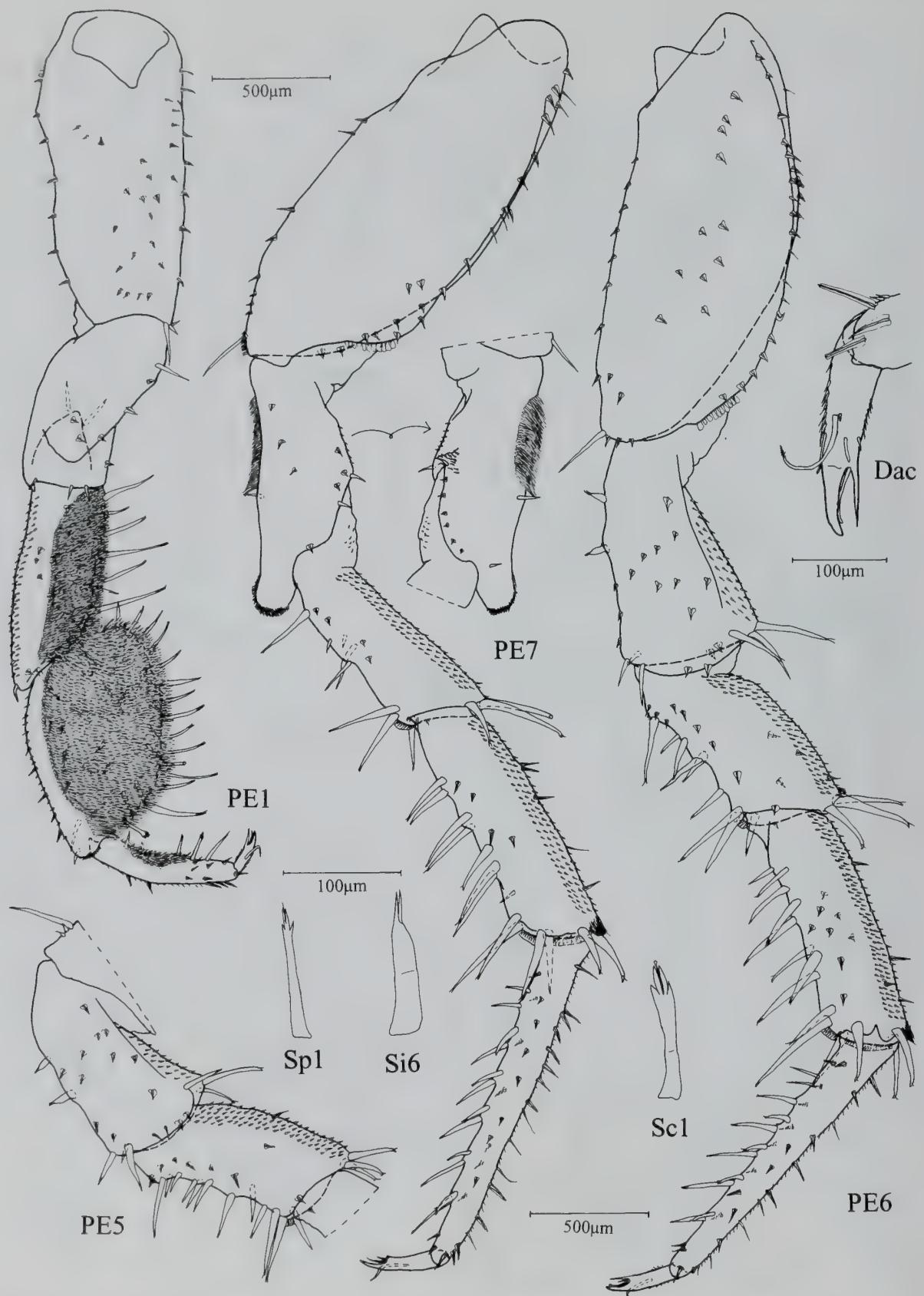
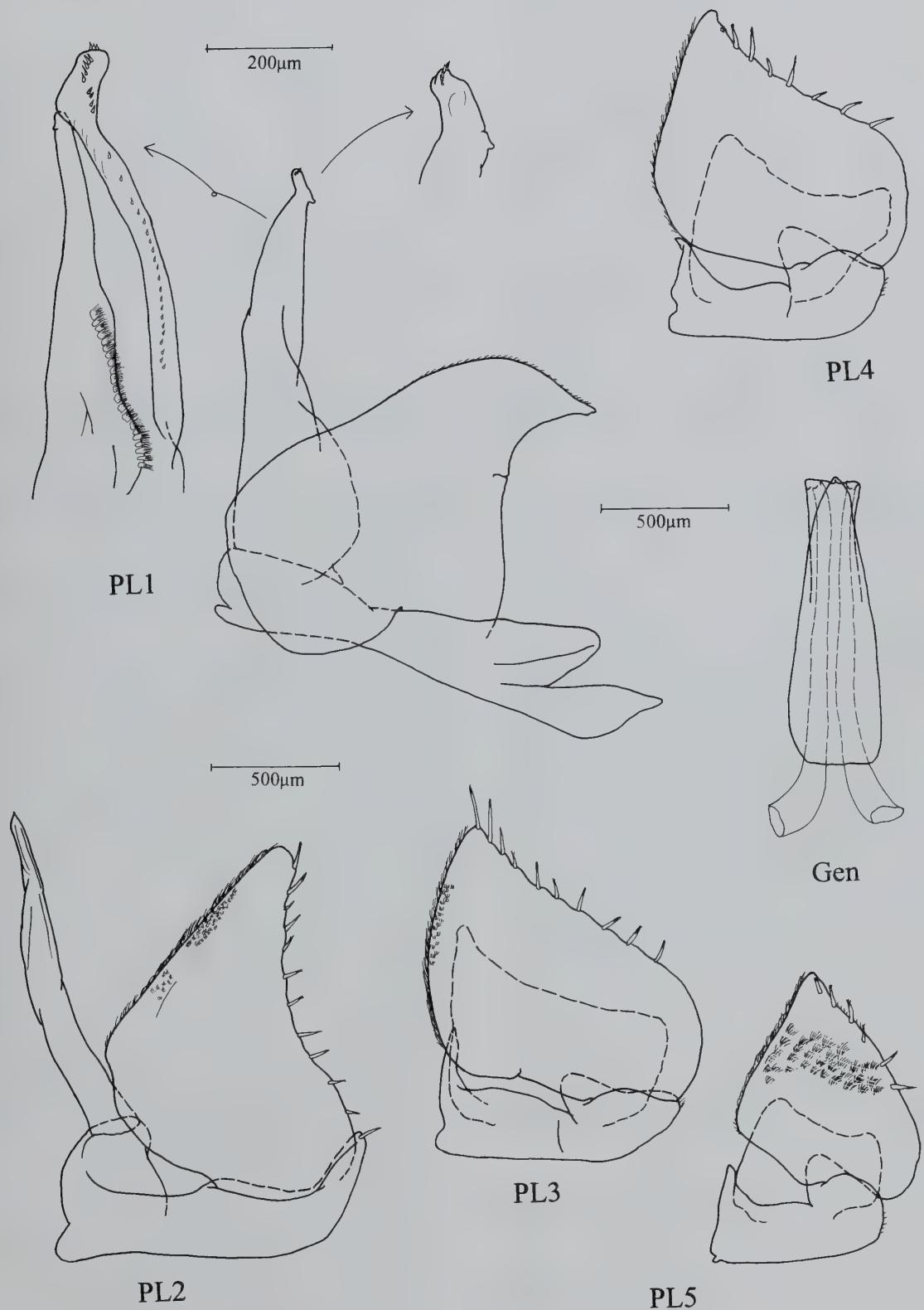


Fig. 23 *Ischioscia trifasciata* sp.nov. Holotype, male 13 mm. Dac dactylus 1 in rostral view; PE1 pereopod 1 in rostral view; PE5–7 pereopods 5 to 7 in caudal view, ischium 7 in rostral view; Sc1 ornamental sensory spine of carpus 1; Si6 sensory spine of ischium 6; Sp1 distalmost sensory spine of propodus 1.



**Fig. 24** *Ischioscia trifasciata* sp.nov. Holotype, male 13 mm. Gen genital papilla; PL1–5 pleopods 1 to 5, rostral view, with detail of endopodite 1 in rostral and caudal view.

**Pereopods.** Slender and long (Fig. 23, PE1–7), dactylus with simple dactylar seta, apically with some rudiments of plumes, long inner claw (Fig. 23, Dac), pereopod 1 carpus with antenna-grooming brush and ornamental sensory spine with hand-like apex (Fig. 23, Sc1), distal sensory spine of basis long. Sexual differentiation. Male pereopods 1 to 3 with setal brushes on propus to merus, carpus enlargement subequal in all 3 pereopods, merus of pereopod 5 and 6 with set of sensory spines of different length, proximal spine of merus 6 on a slight hump, directed distally, pereopod 7 merus medially with proximal sensory spine, two long spines on halflength, two shorter ones more proximally, ischium with dense setal brush, medio-distal lobe with dense cover of small cuticular trichiae, rostrally with a slight depression.

**Pleopods.** Pleopod endopodites slightly bilobate, exopodites with up to 10 sensory spines laterally and minute pectinate scales medially, protopodites 3 to 5 without lateral rudiments of epipodites, no respiratory areas discernible (Fig. 24, PL1–5). Sexual differentiation. Male pleopod 1 exopodite triangular with long lateral point, lateral margin straight, small wrinkle proximally of point, endopodite slender with short subapical protrusion laterally, apex drawn out with 5 spines rostrally, caudally with dense row of spines. Pleopod 2 exopodite with sinuous lateral margin, endopodite with slightly pointed apex.

**Uropod.** As in generic diagnosis.

**Genital papilla.** Ventral shield only slightly surpassing terminal spatula (Fig. 24, Gen).

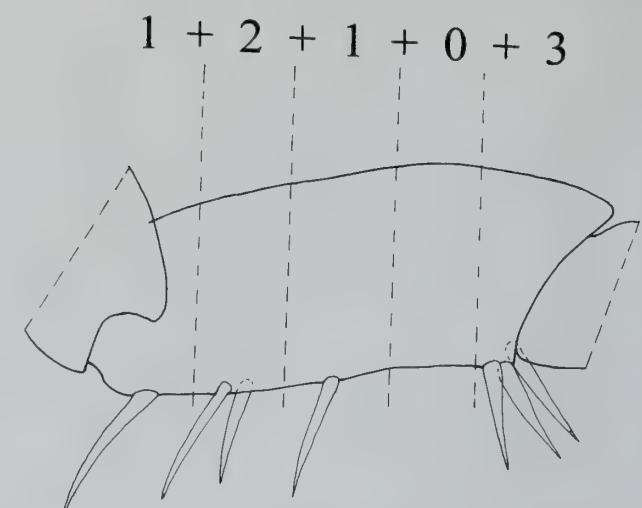
## DISCUSSION

Most of the species of *Ischiopsis* Verhoeff, 1928 found in Venezuela belong into the vicinity of the well-known *I. variegata* (Dollfus, 1893). For a detailed description of this species cf. Leistikow (1997). *I. fasciifrons* sp.nov. is distantly related to the others; it differs in the lack of a setal brush on the male pereopod 7 ischium which bears a transverse furrow medio-rostrally instead of this brush, the distal lobe is rather inconspicuous. Another autapomorphy of this species is the simple dactylar seta instead of an apically plumose one. The apex of the male pleopod 1 endopodite is obtuse with a set of very small spines terminally, quite distinct from the medio-caudal row of spines, the exopodite is only slightly incised, with a short protrusion. The structure of the male pleopod 1 is similar to *I. colorata* sp.nov. from the coastal region of Caracas, this species differs in the presence of prominent setal fields in the carpus and merus of pereopod 4, merus of pereopod 5 and a setal brush on the ischium of pereopod 7. Thus, *I. colorata* is a member of the *variegata*-group of species as defined by Leistikow (1997). This species is further characterized by the shape of the apex of male pleopod 2 endopodite, which is an autapomorphy for the species. The maxillula bears a single subapical tooth like *I. hirsuta* sp.nov., and *I. fasciifrons* sp.nov., this is in contrast to the two teeth in *I. pariae* sp.nov., *I. guamae* sp.nov., and *I. trifasciata* sp.nov.

In *I. trifasciata*, both teeth are apically serrate while in the others the teeth are acute. Besides, the simplified dactylar seta, the shape of the male pleopod 1 and the setation of male merus 7 are autapomorphies of *I. trifasciata*.

*I. hirsuta* is characterized by the following derived character states: a long-haired setal brush on male ischium 7, a hand-like subdistal sensory spine of propus 1, and the long tricorn-like setae on the pereonites.

For *I. guamae*, the most distinct character is the setation of the male merus 7, with the four sensory spines all in the proximal half of



**Fig. 25** Schematic drawing of the male merus 7, indicating the position of sensory spines along medial margin in the ground pattern of the *variegata*-group within the genus *Ischiopsis* Verhoeff, 1928.

the article, one of the smaller stands alongside the long proximal sensory spine. Another autapomorphic character is the caudolateral position of the remainder of the row of spines on the male pleopod 1 exopodite.

The autapomorphies for *I. pariae* are the peculiar shape of the dactylar seta with club-like apex instead of the feathery one, and the reduction of the number of sensory spines on the male merus 7 to three along the medial border.

The setation of the male merus 7 allows easy recognition of the Venezuelan species of *Ischiopsis*. In the ground pattern of the male merus 7, the arrangement of sensory spines along the medial margin from proximally to distally is a long proximal one, two smaller ones distally of the former, another sensory spine even more distally and then a gap which is terminated distally by the medio-distal set of about three long sensory spines, described by the formula [1+2+1+0+3] which can be found in e.g. *I. martiniae* Leistikow, 1997, *I. plurimaculata* Leistikow, 1999 or *I. bolivari* Vandel, 1968 (fig. 25). This formula is varying in the different species of Venezuela as follows:

<i>I. hirsuta</i>	[1+(1+2)+(1+2)+1+3]
<i>I. colorata</i>	[1+2+1+1+3],
<i>I. pariae</i>	[(1+1)+0+1+0+3]
<i>I. guamae</i>	[(1+1)+1+1+0+3]
<i>I. trifasciata</i>	[1+1+3+0+3]
<i>I. variegata</i>	[0+(1+1)+0+0+3].

*I. fasciifrons* does not fit this scheme as it differs in other characters as stated above. The position of the long spine alongside a single short one may be a synapomorphy of *I. pariae* and *I. variegata*, this assumption is supported by the similar shape of the genital papilla, which in both species has a long pointed ventral shield – much longer than the terminal spatula with the laterally placed orifices.

From an ecological point of view, the genus *Ischiopsis* is adapted to many different types of habitat. The autochthonous habitat is the moist rain forest but the members of this genus have adapted to secondary growth, cattle pastures and other disturbed environments. An interesting behavioural difference has been observed in *I. pariae* and *I. variegata* both of which are capable of jumping. The former was observed to jump about 5 cm; *I. variegata* can jump even wider, up to 20 cm and hence can easily escape predators like spiders and



**Fig. 26** Distribution of the species of *Ischioscia* Verhoeff, 1928 in Venezuela. □, *I. guamae*; \*, *I. pariae*; ♦, *I. colorata*; #, *I. trifasciata*; ●, *I. hirsuta*; +, *I. fasciifrons*; ☀, *I. variegata*.

even the astonished human collector. The strong pereopods 6 and 7 with the powerful musculature in the basis are essential for this type of locomotion. The jumping capability may provide another synapomorphy for the two species. Another strategy to escape predators was observed in *I. hirsuta*. A specimen which was observed at the bank of a small brook fled under water and stayed submerged for a considerable period.

These new records widen our knowledge on the genus particularly with respect to their biogeography. The genus is well-distributed in Costa Rica (Leistikow 1999), most records from Venezuela refer to the most abundant species *I. variegata*, which is distributed in the areas adjacent to the Caribbean Sea and also in the interior of Venezuela along the western Corilleras (Fig. 26). The other species seem to have more restricted ranges: *I. pariae* is confined to the Península de Paria; *I. colorata* was found in the vicinity of Distrito Federal. These patchy distributions may be collection artifacts. But they may reflect a characteristic biogeographical pattern found in many Neotropical taxa. Cracraft (1985) argued for the generality of areas of endemism in South America. It is possible to compare distributional data obtained from such diverse taxa as plants (Prance 1982), butterflies (Whitmore & Prance 1986) or birds (Haffer 1974, Cracraft 1985). They all support distinct regions of high endemism called Pleistocene refuges by Haffer (1974). The distribution of species of *Ischioscia* in Venezuela also corresponds to those regions.

*I. pariae* is found in the Parian centre, *I. colorata* in the Venezuelan Montane centre and *I. hirsuta* in the Meridian Montane centre. The widespread *I. variegata* might be an expansive species best adapted to human habitats, although some of the records may be erroneous (Arcangeli 1930, Richardson 1914). *I. variegata* may occur in close spatial vicinity of a second species of *Ischioscia*, but they were not encountered in exactly the same locality. Thus, effective isolation mechanisms have to be postulated to separate the species.

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# A review of the genus *Erenna* Bedot, 1904 (Siphonophora, Physonectae)

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**SYNOPSIS.** The status of the poorly known physonect genus *Erenna* is reviewed in the light of the collection, by submersibles, of specimens in excellent condition. The few previous descriptions had been based on only the tentacles, or on other parts in poor condition. Two species have been described, *E. richardi* Bedot, 1904 and *E. bedoti* Lens & van Riemsdijk, 1908, and there has been some debate as to whether they are conspecific or not. It is concluded here that they are conspecific. Two further *Erenna* species, *E. laciniosa* sp.nov. and *E. cornuta* sp.nov., are described, together with a third, closely related species, *Parerenna emilyae* sp.nov. The distinctiveness of their tentilla, with uncoiled hypertrophied cnidobands, and the nectophores with a basic ridge pattern and a muscle-free zone at the apex of the nectosac, is considered sufficient to warrant the transference of these species into a new physonect family, the Erennidae.

## INTRODUCTION

Very little is known about the physonect genus *Erenna*, and specimens have rarely been identified. In fact, the first species, *E. richardi* Bedot, 1904, was originally described from only six tentacles found attached to the rope of a fish trap brought up from a depth of 5310 m somewhere between Portugal and the Azores. However, these tentacles bore highly distinctive tentilla of a type not previously known for any siphonophore, with uncoiled, hypertrophied cnidobands (stinging bands), and with the gastrodermal walls of the gastrovascular cavity packed with dark granules. Bedot (1904) made a detailed histological study of these tentilla and suggested that they probably belonged to a physonect siphonophore.

A second species, *Erenna bedoti* Lens & van Riemsdijk, 1908, was described from a denuded specimen collected during the Siboga Expedition. From the fragmented material, with many appendages containing black pigmentation, Lens and van Riemsdijk (1908) deduced that the species was a physonect siphonophore, and they assigned it to the family Forskaliidae. Although they could compare only the tentacles and tentilla with Bedot's (1904) material, they reasoned that their material could be referred to a different species because the free end of the cnidoband, on the more developed tentilla in their material, lay proximally, whereas it was distal in *E. richardi*. However, most subsequent authors have considered *E. bedoti* to be conspecific with *E. richardi*.

Bigelow (1911, p. 271) mentioned another specimen of *Erenna richardi*, in poor condition: 'In fact the condition is so bad that it is impossible to state whether or not it is specifically identical with the "Siboga" example. Nor, for that matter, is it clear whether the latter is distinct from Bedot's *E. richardi*'. However, he, like Lens and van Riemsdijk (1908), considered that its closest relatives were the forskaliids. Moser (1925) described a further specimen collected in the Bay of Biscay, which consisted of only a poorly preserved siphosome. She noted that the gastrozooids appeared not to have a pedicle (stalk), and that their gastrodermal lining contained black granules. On the basis of the structure of the gastrozooids and tentacles she considered that it could not be a forskaliid siphonophore and she likened it to a bathyphysid (Order Cystonectae), but noted that the latter lacked nectophores.

Tentacles, with characteristic tentilla were collected, in the north-east Atlantic on two further occasions (Leloup, 1936), but then no

further specimens of *Erenna* species were recorded until Totton (1965) found three more. These were all in poor condition, but sufficient for the mature nectophores and bracts to be described and illustrated for the first time. The apex of the nectosac of the large, flattened nectophores was found to be muscle-free; and the radial canals could have more or less well-developed 'horn' canals ascending into the mesogloea. The bracts were said to have two pairs of lateral processes.

Margulis (1969) added to the description of the nectophores of *Erenna richardi*, noting that there were two small processes on the ventral side of the thrust block (the central region that abuts the stem) and that 'horn' canals were not always present on the lateral radial canals. In a later paper (Margulis, 1977) she described this specimen in more detail and concluded, from the shape of the mature tentilla, that it could be referred to *Erenna richardi*. However, she then briefly discussed possible differences from Lens and van Riemsdijk's (1908) specimen and concluded that *E. bedoti* was also a valid species. Margulis (1990) used these differences to describe a further specimen of *E. bedoti* collected in the southern Pacific. Recently, other specimens of *E. richardi* have been briefly described and/or recorded (Pugh, 1975; Musayeva, 1976; Alvariño, 1980; Leloup, 1980; Daniel, 1985).

In recent years, specimens of *Erenna* species have been collected by the submersibles Johnson-Sea-Link (JSL) I and II, and these are here used to give a more detailed description of *E. richardi*, together with descriptions of two other, previously undescribed, species that can be referred to the same genus. In addition, another JSL specimen, that is closely related to the genus *Erenna*, will be described. The taxonomic status of these species is discussed below and it is concluded that they should be separated off into a new family. The validity of *E. bedoti* also is discussed.

### Family ERENNIDAE fam. nov.

**DIAGNOSIS.** Physonect siphonophores best characterised by their uncoiled tentilla bearing a hypertrophied cnidoband with nematocysts of three types: large anisorhizas and two types of smaller ones (? haplonemes). Terminal process devoid of nematocysts. Nectophores with basic ridge pattern of apico-, infra- and vertical laterals; with apical muscle-free zone on nectosac; radial canals straight or slightly curved. Ostium, without mouth plate, opening basally.

Pneumatophore without apical pore. Gastrozooids without pedicle. Dioecious.

**REMARKS.** As noted in the Introduction, both Lens and van Riemsdijk (1908) and Bigelow (1911) considered the genus *Erenna* might be related to the physonect family Forskaliidae, whereas Moser (1925) associated it with bathyphysid cystonects. However, Totton (1965) placed *Erenna* in the physonect family Agalmatidae. As Pugh (1998) discussed, the Agalmatidae is probably a composite family containing all those species that do not have the distinctive characters of other physonect families. There is a core of similar genera, *Agalma*, *Halistemma* and *Lychnagalma*, which have involucrate tentilla, with tightly coiled cnidobands. *Nanomia* is somewhat similar. However, the other genera are often difficult to relate to each other in any basic way.

Pugh (1999) discussed this further, with regard to the genus *Bargmannia*, which Totton (1965) had placed in the family Pyrostephidae. Among the key characters used in establishing the taxonomic position of that genus were the ridge pattern on the nectophores; the presence of a muscle-free zone on the nectosac; and the structure of the tentillum. With regard to the ridge pattern, which consisted of pairs of apico-, infra and vertical (meso-) laterals, he noted that a similar arrangement was found on the nectophores of *Pyrostephos vanhoeffeni* Moser, 1925 and *Erenna richardi*; with an even simpler arrangement, omitting the vertical laterals, being found in *Marrus* species. Similarly, all these species had a muscle-free zone on the nectosac. In addition, *Bargmannia* species, *P. vanhoeffeni* and *M. antarcticus* were known to be dioecious, whereas most other physonects are known to be monoecious. In the present study it will be shown that two *Erenna* species are dioecious, with monovan gonophores; while gonophores were not found with the other two species. These characters separate these four genera from all other agalmatids.

In *Bargmannia* spp., *Pyrostephos vanhoeffeni* and *Marrus* spp. the tentilla have simple, straight, or loosely coiled, cnidobands; with long contractile terminal filaments bearing nematocysts. However, *Erenna richardi* has a straight, hypertrophied cnidoband; and a rigid terminal process devoid of nematocysts. There are also differences in the types of nematocysts present on the tentillum. For many agalmatids four types are present: homotrichous anisorrhizas (haplonemes), and either mastigophores or stenoteles on the cnidoband; desmonemes and acrophores in the terminal filament. The tentillum of *Marrus* species appears to conform with this pattern, with microbasic mastigophores included in the cnidoband. In *Bargmannia* species and *P. vanhoeffeni* large nematocysts, probably stenoteles, were present only on the proximal part of the cnidoband; with two types of smaller nematocysts present throughout the remainder of the cnidoband and terminal filament. Pugh (1999) was uncertain whether the latter were acrophores or desmonemes, but haplonemes were thought to be absent. As is shown below, the cnidobands of *Erenna* species contain mastigophores and two types of haplonemes; but, as noted above, there are no nematocysts on the terminal process.

Pugh (1999) concluded that there were sufficient similarities between *Bargmannia* spp. and *Pyrostephos vanhoeffeni* to retain the former in the family Pyrostephidae. However, despite the similarities of the nectophoral ridge pattern and the muscle-free zone on the nectosac, there are certain marked differences between these species and those of the genus *Erenna*. This particularly applies to the structure of the tentillum and its nematocysts; but also to the general structure of the nectophore. Pyrostephid nectophores have a large triangular thrust block and the axial wings are either reduced or absent; with the lateral radial canals on the nectosac arising separately

from the dorsal canal. In *Erenna* spp. the thrust block is much smaller, while the apical wings are well-developed, and all four radial canals arise from the pedicular canal either together, or very nearly so. In addition, palpons with palpacles (reduced tentacles) are present in *Erenna* species, while they are totally absent in *Bargmannia* spp., or highly modified into palpacle-less oleocysts in *P. vanhoeffeni*. Also the female gonophores of the pyrostephids contain more than one ovum, while those of *Erenna*, where known, are monovan. These differences are here considered to be sufficient differences to warrant the establishment of a new family for the *Erenna* and closely related species described herein. The exact status of the genus *Marrus* remains uncertain, as Pugh (1999) discussed.

## *Erenna* Bedot, 1904

*Erenna* Bedot, 1904: 10–14.

**DIAGNOSIS.** Nectophores dorso-ventrally flattened with tapering axial wings; apico- and infra-lateral ridges respectively form upper and lower margins of lateral surface, with short, perpendicular, vertical lateral ridge connecting them. Lateral radial canals straight, thickened on apico-lateral margins of nectosac; with or without additional small protuberances, spikes, or ‘horn’ canals. Bracts of two types, both with patches of epidermal cells, including nematocysts, on dorsal swelling at distal extremity. Tentillum large, with hypertrophied, uncoiled cnidoband, and rigid terminal process devoid of nematocysts. Gastrozooid with large swollen basigaster, but no obvious pedicle.

## *Erenna richardi* Bedot, 1904

*Erenna richardi* Bedot, 1904: 10–14, Pl. II, figs. 1–12

*Erenna bedoti* Lens & van Riemsdijk, 1908: 66–69; Margulies, 1977: 148–151, 1990: 138–142.

**MATERIAL EXAMINED.** The description is based largely on a specimen collected during Johnson-Sea-Link (JSL) II Dive 1456 (2 xi 1987; 24° 00.9'N 82° 15.7'W; depth 871 m). In addition, parts of another large specimen collected during JSL I Dive 2889 (19 xii 1990; 26° 22.3'N 78° 46.2'W; depth 701 m) have been examined. These parts have been donated to The Natural History Museum, London, where they are registered as BMNH 2000.1819. Unfortunately, the remainder of the specimen, including the siphosome, has dried up.

**DIAGNOSIS.** Nectophores large, flattened, with prominent apico-, infra- and vertical lateral ridges; plus at least two pairs of indistinct and incomplete laterals in basal half; apico-laterals divide close to ostium. Thrust block large with, in mature nectophores, two small digitate protuberances on ventral surface. Radial canals black pigmented; lateral ones with thickened walls in region of lateral margin of nectosac; with small protuberances or spikes. Gastrozooids black pigmented, particularly in greatly expanded basigaster, with two prominent lateral lobes. Tentillum with hypertrophied cnidoband, and long rigid distal terminal process with a diverticular canal and a pair of ‘ocelli’ close to its end.

**DESCRIPTION.** An image (Fig. 1) taken from a video of the *in situ* JSL II Dive 1456 specimen shows the biserially arranged nectophores and the contracted siphosome.

**PNEUMATOPHORE.** Pneumatophore ovoid, measuring 7 by 4 mm. Margulies (1977) noted the presence of eight vertical septa on her specimen, but these were not visible on the present material.

**NECTOPHORE.** (Figs 2 & 3). About 45 nectophores, at various



**Fig. 1** *Erenna richardi*. Image from *in situ* video of JSL II Dive 1456 specimen; approximately 70–80 cm in length.

states of development, and several nectophoral buds, remained with the JSL II 1456 specimen. They were flattened, and measured up to 32 mm in length, 33 mm in width and 10 mm in height. The large axial wings tapered toward their apices (Fig. 2A *aw*). Mature nectophore had relatively large thrust block (Fig. 2C *tb*) with a broad U-shaped indentation apically. On its ventral surface there were two small conical protuberances (Fig. 2C *cp*). However, on the younger nectophores, the thrust block was small and had no protuberances (Fig. 3).

The prominent main ridge system consisted of pairs of apico- (Fig. 2A *ral*) and infra-laterals (Fig. 2B *ril*), which united close to the apex of each axial wing; and a pair of vertical laterals (Fig. 2B *rvl*) that connected the apico-laterals with the infra-laterals; although in some nectophores the junction with the latter was weak

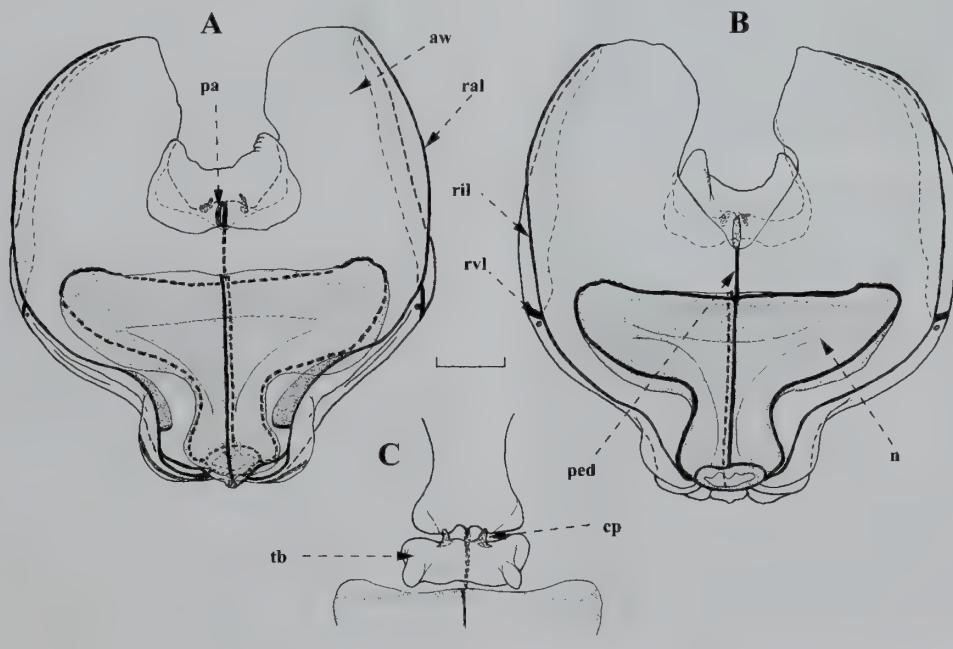
and difficult to discern. Apico-laterals branched close to the ostium, with each branch reaching the latter. In addition to these ridges at least two pairs of incomplete lateral ridges passed obliquely down the lateral facet in the basal half of the nectophore. Often these were difficult to discern without staining, but were also described by Margulies (1977), who noted 2–3 pairs of them.

Ostial opening basal with no obvious mouth plate. On each side of the ostium there were prominent lateral protuberances on which lay strips of distinctive epidermal cells. A much smaller triangular patch also was present dorsally. In addition, there was a small patch of such cells on each side of the nectophore, at about the mid-height of, and basal to, the vertical lateral ridges. All these patches of epidermal cells are believed to be sites of bioluminescence.

T-shaped nectosac (Fig. 2B *n*) with a distinct muscle-free area across the whole of its apical region. Pallial canal (Fig. 2A *pa*) was relatively short, running from the base of the thrust block over onto the ventral surface and ending just beyond the point of origin of the pedicular canal (Fig. 2B *ped*). On the nectosac the pedicular canal typically gave rise to all four radial canals, although occasionally there was a slight asymmetry in the arrangement. All four radial canals were straight. Laterals pass out, through the muscle-free zone, toward the lateral margins of the nectosac. Typically, before reaching the latter, they became thickened and could have small protuberances, or spikes extending up from them. These thickenings were particularly prominent on the youngest nectophores. All the canals had brown, but originally black, pigment in their gastrodermal walls.

**SIPHOSOME.** As the *in situ* video (see Fig. 1) showed, the siphosome was tightly contracted, and possibly, as in *Agalma okeni* Eschscholtz, 1825 and *Frillagalma vityazi* Daniel, 1966 (see Pugh, 1998), this was its permanent state.

**BRACT.** (Fig. 4). Two types of bract were present; the first long, up to 50 mm, and narrow (Fig. 4A); the second shorter and broader (Fig. 4B, C). Both possessed a pair of prominent, lateral cusps. These



**Fig. 2** *Erenna richardi*. **A.** upper and **B.** lower views of mature nectophore. **C.** detail of folded back thrust block. Scale bar 5 mm. *aw* axial wing; *cp* conical protuberance; *n* nectosac; *pa* pallial canal; *ped* pedicular canal; *ral*, *ril*, *rvl* apico-, infra- and vertical lateral ridges; *tb* thrust block.

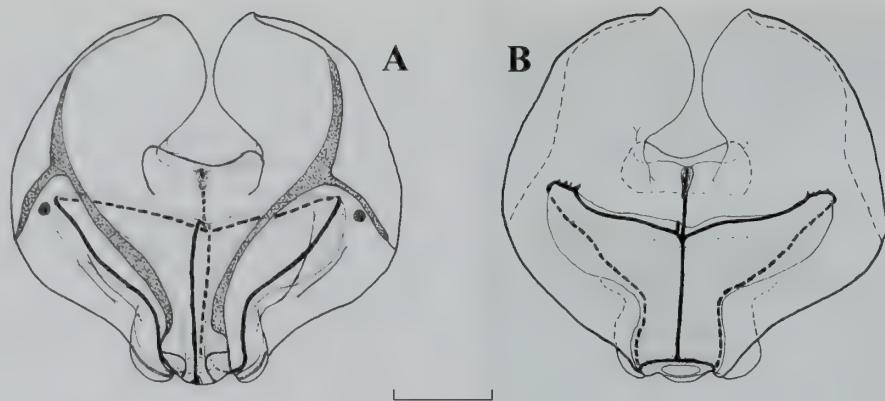


Fig. 3 A. upper and B. lower views of young nectophore. Scale bar 5 mm.

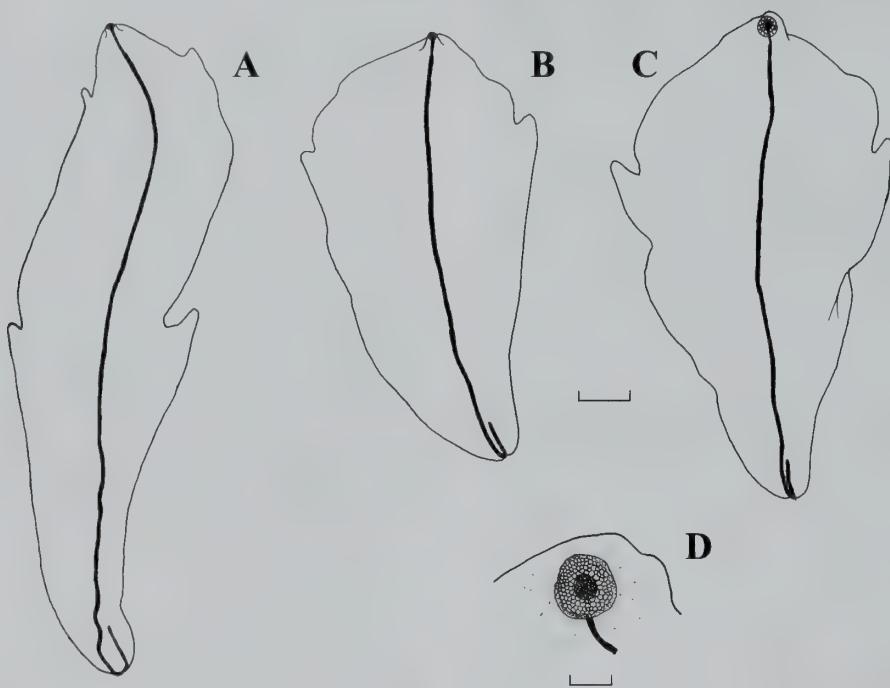


Fig. 4 *Erenna richardi*. A. first and B., C. second types of bract. D. detail of distal end of a bract. A–C. scale 2 mm; D. scale 0.2 mm.

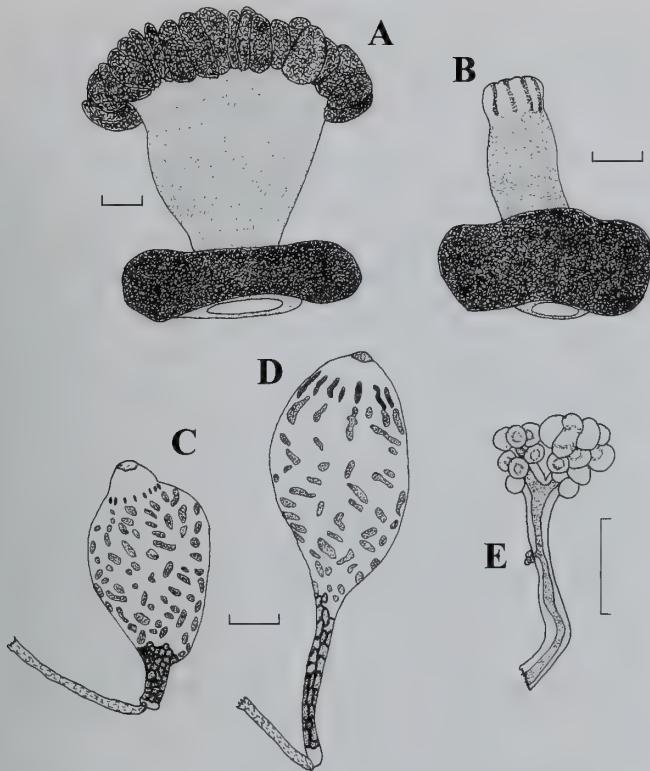
were situated in the distal half of the second type of bract, but in the first type they were positioned at about 13–14 mm from the proximal end of the bract, whatever the length of the latter. Thus in the longest bracts they were situated at about one quarter to one third its length; whereas in smaller ones they could be positioned in the distal half of the bract. Longer bracts of the first type had a second pair of lateral cusps close to the distal end. For both types, the bracteal canal originated, proximally, on the dorsal surface of the bract. For most of its course it remained in close contact with the ventral wall of the bract and there were striated bands of cells on each side of it. Close to the distal end of the bract it penetrated through the mesogloea to terminate below a small cup-shaped clump of large epidermal cells sunk into the dorsal surface at the tip of the bract (Fig. 4D). Some of these cells in this clump probably produced bioluminescence; others were nematocysts measuring c.  $68 \times 24 \mu\text{m}$ . No patches of such epidermal cells were noted elsewhere on the bract.

**GASTROZOOID.** (Fig. 5 A, B). Large gastrozooids contained dark brown (black in life) pigment. The proboscis region often was

widely open and folded back on itself exposing a mass of villi. Enormous basigaster with two large lateral lobes, and also expanded, to a lesser extent, on the side opposite to where the tentacle was attached. No obvious pedicle.

**TENTACLE AND TENTILLUM.** (Figs 6, 7). Bedot's (1904) original description and illustrations of the tentacle and tentilla were detailed and accurate, and need little elaboration. The annulated tentacle had a muscular lamella running down one side, with the tentilla attached on the opposite side, at the internodes.

Each tentillum consisted of a pedicle (Fig. 7p), a cnidoband (Fig. 7c) and a terminal process (Fig. 7p). The largest tentilla (Fig. 6) have a pedicle of up to 4–5 mm; longer than Bedot described. However, no doubt its length can be varied in life, and photographs of the specimen before preservation showed the pedicle to be highly contracted. The cnidoband measured up to c. 15 mm long and was laterally compressed. It consisted of the cnidoband proper, where the nematocysts are attached, and what Totton (1965) called, in the case of *Pyrostephos vanhoeffeni* Moser, 1925, the saccus (Fig. 7s).



**Fig. 5** *Erenna richardi*. A. and B. Gastrozooids; C. and D. palpons; E. Immature gonodendron. Scale 2 mm.

The bulk of the saccus was made up of a thick layer of transparent gastrodermal cells which formed a characteristic reticulate pattern (Fig. 6), through which the narrow, dark (black in life) pigmented gastrovascular canal (Fig. 7gvc) passed. In many preserved tentilla this canal was damaged. Figure 6 shows an undischarged and a discharged tentillum.

The numerous nematocysts formed a dense, darkly pigmented cnidoband, the sides of which undulated irregularly. On the mature tentillum the distal end of the cnidoband hung free from the main body. Three types of nematocysts were present. On the sides there were rows of larger ones, probably homotrichous anisorhizas, measuring c.  $165 \times 32$   $\mu\text{m}$ . Between these were numerous smaller nematocysts of two types, one measured c.  $43 \times 15$   $\mu\text{m}$ , the other c.  $27 \times 20$   $\mu\text{m}$ . No discharged nematocysts of these types were found, but probably they were both atrichous haplonemes, as Margulies (1977) suggested, although she noted only one type.

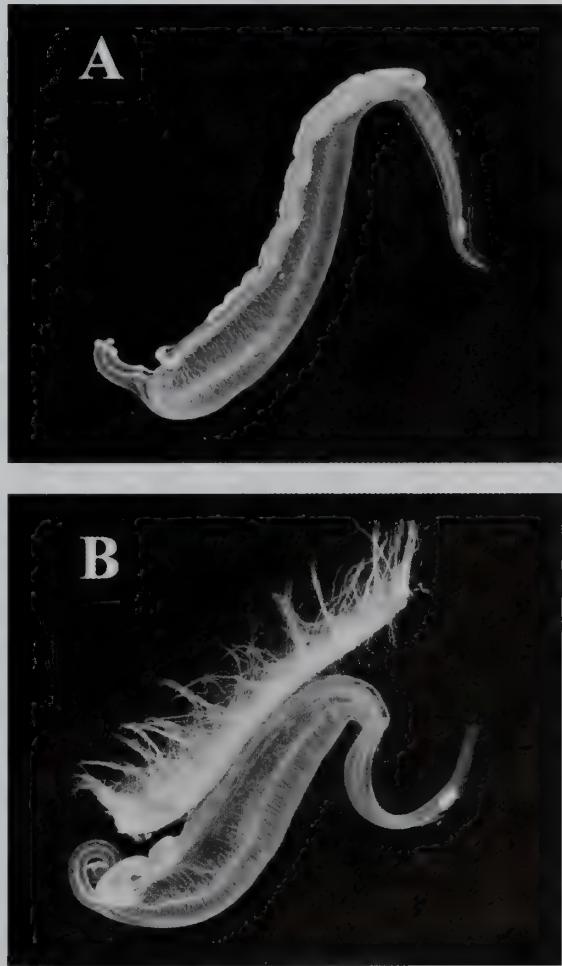
The rigid terminal process (Fig. 6) was up to c. 10 mm in length and devoid of nematocysts. The gastrovascular canal passed through it, ending close to its distal extremity. Just proximal to the end of the canal it branched off a diverticular canal (Fig. 7dc) that passed back through the terminal process to end below the distal part of the cnidoband. As Bedot (1904) noted there was a band of longitudinal musculature on each side of the terminal process. Overlying the lateral sides of the diverticular canal, close to its point of origin, there was a pair of brownish-white oval structures (Fig. 7o) comprised of distinctive epidermal cells. Lens & van Riemsdijk (1908) aptly called them 'ocelli', as is discussed below.

As noted above it was the distal end of the cnidoband that hung free from the main body of the mature tentillum. However, on the young, developing tentillum (Fig. 7A), the cnidoband formed a triangular process that was slightly undercut on its proximal surface;

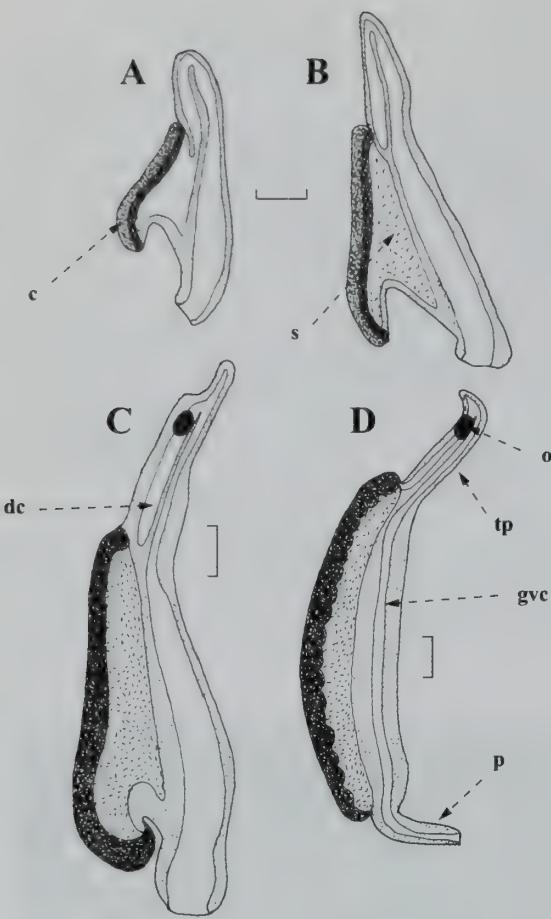
with the pedicle and terminal process being only slightly developed. The axial and diverticular canals were prominent, and the latter opened into the saccus of the cnidoband. With further development, the saccus became closed off and began to fill with gastrodermal cells (Fig. 7B). The cnidoband remained undercut proximally. With further elongation of the tentillum (Fig. 7C, D), the proximal part of the cnidoband began to fuse with the saccus, and the 'ocelli' on the terminal process were developed, while the canal system narrowed. Finally, the distal end of the cnidoband became detached from the saccus.

**PALPON.** (Fig. 5C, D). Up to 15 mm in length, with a palpacle attached at the base of the pedicle. Brown (black in life) pigment throughout. Pedicle with reticulate pattern of cells. Main stomach region with an irregular pattern of patches. Distally these were concentrated to form 12–14 vertical stripes, with denser pigmentation, surrounding the base of the proboscis with its terminal opening. No obvious nematocysts present on the palpacle.

**GONODENDRA.** (Fig. 5E). Only female gonodendra were found on the JSL II 1456 specimen. Mature female gonodendra were comprised of small, tightly packed bunches of c. 20–25 gonophores, with a milky brown coloration, connected to a relatively short stalk. Each gonophore measured c. 0.45 mm in diameter and contained a single



**Fig. 6** *Erenna richardi*. Photographs of tentilla (c. 25–30 mm in length) before (A.) and after (B.) discharge of nematocysts.



**Fig. 7** *Erenna richardi*. **A–D.** Early stages in the development of a tentillum. Scale 0.5 mm. *c* cnidoband; *dc* diverticular canal; *gvc* gastrovascular canal; *o* 'ocellus'; *p* pedicle; *tp* terminal process.

egg. The immature gonodendra (Fig. 5E) were more darkly pigmented and had a relatively long stalk which typically bifurcated close to its apex, with the gonophores being developed on the branches. One of these branches could be denuded and could be mistaken for a gonopalon. Occasionally small gonophores were budded off approximately half way up the stalk. No gonophores were found with the JSL I Dive 2889. However, two specimens from the *Discovery* collections also bore only female gonodendra.

**DISTRIBUTION.** Of the four specimens of *Erenna richardi* collected by the JSL submersibles, one came from the vicinity of the Dry Tortugas, between Florida and Cuba; two from The Bahamas; and one from c. 27°N 85°W in the Gulf of Mexico (Rebeca Gasca – personal communication). The species also has been found occasionally in recent *Discovery* collections in the North Atlantic, mainly south of 35°N and at depths greater than 1000 m. Much of the material is in too poor a condition to identify to species, although it seems likely that the presence of black pigment in the radial canals of the nectophore is specific to *E. richardi*. However, one large specimen, comprising 34 nectophores, over 400 bracts and several stem pieces, from *Discovery* St. 8599 (c. 8°40'N 23°14'W; depth 3000–3500 m), clearly is *E. richardi*; as is a specimen from St. 10157#3 (31°3.6'N 13°W; 650–1000 m). In addition some damaged nectophores that can be referred to this species have been collected by four hauls fished c. 300 m above the bottom in the proximity of the 'Rainbow' and 'Lucky Strike' vents on the Mid-Atlantic Ridge (c.

37–38°N, 32–33°W; depth range 1793–2613 m). Better preserved material has also been collected recently in the vicinity of the East Pacific Rise (c. 12°50'N, 104°W) at depths of about 2500 m. The siphosome of one of these specimens bore numerous female gonodendra.

Leloup (1980) listed the scant published data on the geographical distribution of *Erenna richardi*, including the conspecific *E. bedoti*. The material described by Bedot (1904), Lens and van Riemsdijk (1908), Bigelow (1911), Moser (1925) and Leloup (1936, 1980) probably can be referred to *E. richardi*; but this is not the case for all of Totton's (1965) material. His figure 38, which is said to be a reconstruction, shows a nectophore with short 'horn' canals arising from the lateral radial canals on the nectosac. Re-examination of the single nectophore, in the NHM collections, shows that incomplete lateral ridges are also present and so it is referred to *E. richardi*. However, the label with it states that the *Discovery* station at which it was collected is St. 4255 not, as Totton stated, St. 2061. The reverse is true for the specimen figured in figure 39. Since figure 39 looks more like a 'reconstruction' than figure 38, it is presumed that the legends to the two figures were accidentally transposed. Totton (1965) mentioned a larger specimen from *Discovery* St. 4230, but this was not found. His other material from La Jolla, California, supplied by Dr Ahlstrom, and the Beebe collections from Bermuda, together with some bracts from *Discovery* St. 4253, which he did not mention, probably can be referred to *E. richardi*, but are in poor condition. The *Discovery* St. ?2061 material, is referred to another species, described below.

Of the other records not included by Leloup (1980) or published more recently, no description was given by Alvariño (1969, 1980) or Musayeva (1976) and so their true identity remains in doubt; particularly since Alvariño (1981) described a specimen that is probably not *E. richardi*. However, as with the description of Daniel (1985), it is difficult to decide whether or not she was largely copying the description and figures of Totton (1965). The two specimens described or mentioned by Margulis (1969, 1977, 1990) can be referred to *E. richardi*, although in the last paper the specimen was described under the name *E. bedoti*. This will be discussed in more detail below. Finally, the record given by Pugh (1975) is based on *E. richardi*.

**BEHAVIOUR.** The JSL II 1456 specimen was briefly observed on board the mother ship after collection. It was noted that the terminal processes of the tentilla were kept rigid and were rapidly vibrated. Meanwhile, the cnidoband might become bent into a U-shape. It has been suggested (Pugh, 1989) that vibration of the terminal process might be an example of aggressive mimicry of a swimming chaetognath. The two 'ocelli' might then be a representation of chaetognath's gonads. Equally, the vibration of the terminal process might be mimicking the swimming behaviour of a larval fish; the two 'ocelli' then representing eyes.

As Totton (1965, p. 76) noted, 'What is so characteristic of *Erenna [richardi]* is the hypertrophy of the cnidoband, which must be a very formidable stinging apparatus'. This has certainly proved to be the case, as was demonstrated when a colleague was painfully stung when he inadvertently came into contact with a tentacle of one of the specimens collected by the JSL submersible.

**REMARKS.** Lens and van Riemsdijk's (1908) description of *Erenna bedoti* was based on two fragments of stem; one being the nectosome, with an apical pneumatophore, and the other a small part of the siphosome. However, they could only compare the tentacles and tentilla with those described by Bedot's (1904) for *E. richardi*. For the tentacle they stated (p. 68) that it 'reminds one exactly of the tentacle described by BEDOT'; and (p. 69) that 'the most mature

tentillum . . . reminds one at once of the tentilla described by BEDOT'. They concluded (p.69) that 'there exists undeniably the closest relationship between the tentacles and tentilla of *Erenna Richardi* and *Erenna Bedoti*.' So why did they separate them? Their earlier logic (p. 66) 'We therefore called this only specimen *Erenna*, using a new species denomination "*Bedoti*" as of course we cannot decide whether the tentacles described by BEDOT belonged to a specimen entirely identical with ours' seems very obscure.

Lens and van Riemsdijk suggested a possible difference between the tentilla of their specimen and that of Bedot. They believed that, in the largest tentillum, the free end of the cnidoband was proximal ('basal') while in *Erenna richardi* it was distal (although they referred to the latter as 'proximal'). They also noted the presence of a small black spot in the distal region of the cnidoband, which they suggested would become the 'ocelli' that Bedot described. However, the 'ocelli' of *E. richardi* are positioned toward the end of the terminal process, even in the developing tentilla (see Fig. 6C, D). Have, then, Lens and van Riemsdijk misinterpreted the structure of their tentilla? Close examination of their illustration (Plate XI, fig. 89) suggests that this is probable. It is suggested that what they call the pedicle is, in actuality, a very deformed terminal process; while the 'apical part' (terminal process) is the pedicle. Then the free end of the cnidoband is distal, as it is in *E. richardi*. For this to be so, the spot, which lay close to the proximal end of the cnidoband, and which they thought was equivalent to the 'ocellus' of *E. richardi*, must be considered an artefact, and that the true 'ocelli' have been destroyed. This is borne out by Lens and van Riemsdijk (1908, p.69) statement that 'Microscopical sections have been made but the material is unfortunately absolutely insufficient, the different layers being all destroyed'. It appears that all the largest tentilla were sectioned as none are now present with the type material. However, some developing tentilla are still present with the holotype and these conform exactly with those of *E. richardi*. Thus, there does not appear to be any concrete evidence to separate specifically Lens and van Riemsdijk's material from that of Bedot.

This conclusion was reached by Totton (1965), who considered *Erenna bedoti* to be conspecific with *E. richardi*. However, Margulis (1977, 1990) resurrected the debate, when she described another specimen of *E. richardi* Margulis (1997). She correctly noted that, on the nectophores, there were two digitate processes on the ventral side of the thrust block, and 2–3 extra ridges on the lower lateral facet. On the siphosome she found, as indeed had Lens and van Riemsdijk (1908), the presence of peculiar muscular outgrowths, but did not know their function. They are, undoubtedly, the remains of the muscular lamellae to which bracts were once attached. One curious feature she described was that one detached tentacle arose from a black-pigmented formation that had a spherical dilation on each side. This was, of course, the basigaster of the gastrozooid, but she failed to appreciate this. The youngest tentillum had a digitate outgrowth in the region that was to become the cnidoband; the oldest were as Bedot (1904) described them. Margulis (1977) then made a brief comparison with Lens and van Riemsdijk's (1908) description of *E. bedoti*. The only differences she noted were that the tentacles of *E. bedoti* lacked the basal outgrowths (i.e. the basigaster), and that their young tentilla did not have a digitate outgrowth.

These points were addressed further by Margulis (1990), when she described fragments of another specimen that she referred to *Erenna bedoti*. The key features by which she distinguished this specimen from *E. richardi* were that:

- a) the thrust block on the nectophore was smaller, with its distal margins stretched into thread-like outgrowths; and that the two

processes on its ventral surface were digitate or papillose, but not lamellate as in *Erenna richardi*;

- b) there were marked differences in the structure of the gastrozoid, and;
- c) the young tentilla of *Erenna bedoti* had an oval outgrowth, while in *E. richardi* it was finger-shaped.

As has been shown above, the size of both the thrust block and the digitate processes varies with the size of the nectophore of *Erenna richardi*, which, as will be seen, is the only erennid species to have such processes. Thus, judging from her illustrations, the damaged condition of Margulis's material is the most likely explanation of the differences she noted. It should be noted, moreover, that black pigment was present in Margulis's material. The differences in the gastrozooids mainly concern the basigaster. Margulis now recognised that, in *Erenna richardi*, this was the large structure, with two large rounded lobes, that she had found at the proximal end of the tentacle. However, such a structure was not found on the larger gastrozooids of her latest specimen; although it was clearly large and inflated on the younger ones. This would be a reasonable difference if Margulis had not given the impression that the basigaster had been destroyed, by describing how its outer coating began to shed until it was completely absent. Personal experience has shown that it is, indeed, easy to destroy the epidermal layers of the basigaster. Finally, the differences between the young tentilla are considered to be mere reflections of their state of growth. The important similarities between Margulis's (1990) material and *E. richardi* are that in both there is a pair of protuberances on the ventral side of the thrust block of the nectophore, and that black pigmentation is present. The former, and almost certainly the latter, of these are characteristics for only *E. richardi* and, thus, it seems inconceivable that *E. bedoti* is nothing more than conspecific with *E. richardi*.

#### *Erenna laciniata* sp.nov.

HOLOTYPE. The specimen from JSL II Dive 1454 is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1821.

MATERIAL EXAMINED. The description is based on two specimens collected by the JSL II submersible during dives 1454 (30 viii 1987; 24°30.8'N 83°45.2'W; depth 811 m) and 1688 (11 x 1988; 26°23.5'N 78°39.5'W; depth 853 m).

DIAGNOSIS. Nectophores large, dorso-ventrally flattened, with only basic ridge pattern; with weak division of apico-laterals close to ostium. Thrust block small, with U-shaped median indentation and ventral flaps, but no conical protuberances. Lateral radial canals only slightly thickened at apico-lateral corners of nectosac. Bracts of two types, with lateral flap, more extensive in one type than the other. Tentilla characteristic, with terminal process arising close to base of cnidoband and bearing two distal 'ocelli'.

#### DESCRIPTION

PNEUMATOPHORE. The pneumatophore measured c. 2.9 × 1.9 mm; gas expansion having ruptured its base. There were no obvious striations or pigment.

NECTOSOME. Each specimen had 50–60 nectophores, which, in life, were arranged biserially.

NECTOPHORE. (Figs 8, 9). Flattened, up to 25 mm in length, 29 mm in width and c. 5 mm in height. Large tapering axial wings. On the mature nectophores (Fig. 8) the thrust block was relatively small and divided into two parts by a median U-shaped indentation.

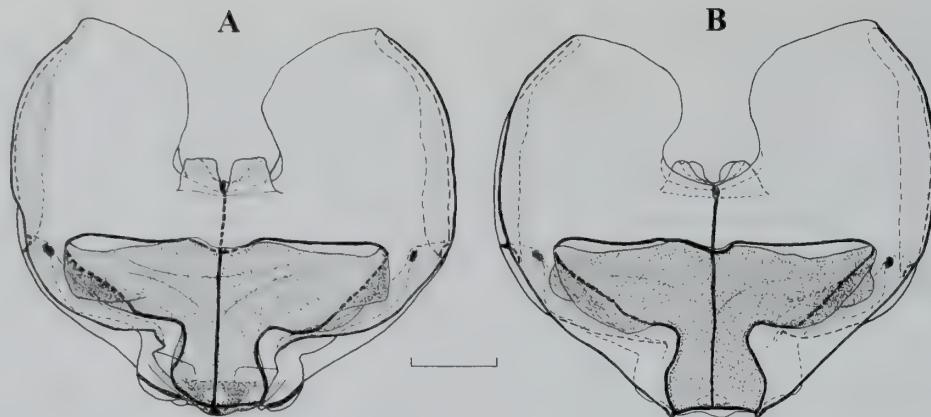


Fig. 8 *Erenna laciniata*. A. upper and B. lower views of mature nectophore. Scale 5 mm.

On each side there was a thickened flap that lay ventrally and was directed toward the mid-line. On smaller, younger nectophores (Fig. 9) the thrust block consisted of two small protuberances separated by a U-shaped indentation.

The main ridge system was well delineated, especially in the younger nectophores (Fig. 9). It consisted of pairs of infra- and apico-lateral ridges, which united close to the lateral apices of the axial wings; and a short pair of vertical laterals connecting them (Fig. 8), although, in younger nectophores, the junction with the apico-laterals was indistinct (Fig. 9). The infra-laterals ended, basally, on either side of the ostium. The apico-laterals remain prominent until just above ostial level. In younger nectophores, close to the ostium, the apico-laterals gave rise to three very vague, but broad branches (Fig. 9A). However, in mature nectophores only after staining could two very vague ridges be discerned (Fig. 8A). These would be virtually impossible to see in damaged or poorly preserved material.

No obvious mouth plate, and ostial opening basal. Prominent protuberances on each side of the ostium which bore strips of distinctive epidermal cells, and another triangular patch in mid-line on dorsal side of the ostium. In addition, a relatively large patch of such cells was present on each side of the nectophore, at about the mid-height of, and immediately basal to, the vertical lateral ridges (Figs 8A, 9A). All these patches are believed to be sites of bioluminescence.

T-shaped nectosac with a distinct muscle-free zone at its apex. Short pallial canal, originating at the base of the thrust block, with a long pedicular canal, which on reaching the nectosac gave rise to the four, straight, radial canals. In the younger nectophores there were obvious signs of thickening of the lateral radial canals in the apico-

lateral region of the nectosac, but these were difficult to discern in the mature ones. No small protuberances, or 'horn' canals, were present. In the JSL material the radial canals had no obvious pigmentation, although in other nectophores, which are tentatively referred to this species, they could have an orange hue.

**SIPHOSOME.** On collection the siphosome of both specimens was tightly contracted. The gastrozooids and the terminal processes to the tentilla were lightish brown in colour; while the palpons were suffused with brown pigment.

**BRACT.** (Fig. 10). Over 1000 bracts, of two types, were found with

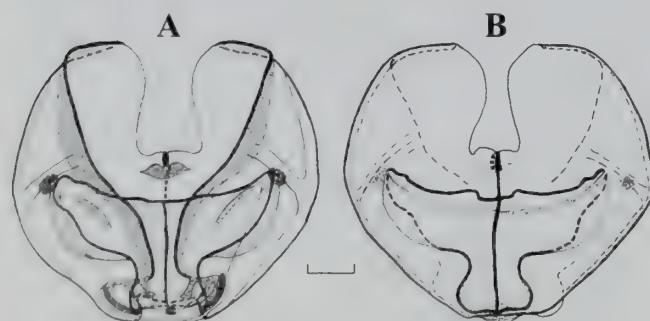
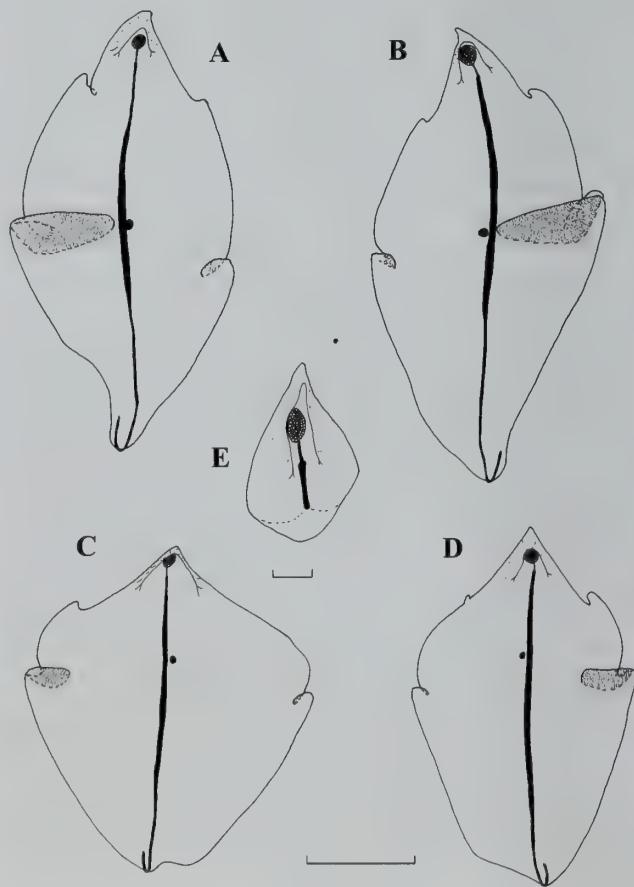


Fig. 9 *Erenna laciniata*. A. upper and B. lower views of immature nectophore. Scale 2 mm.

Fig. 10 *Erenna laciniata*. Bracts. A., B. dorsal views of first type; C., D. dorsal views of second type. Scale 5 mm. E. Immature bract. Scale 1 mm.

the JSL 1688 specimen, occurring as enantiomorphic (mirror-image) pairs. The first type of bract (Fig. 10A, B), which measured up to 25 mm in length, was deeply incised on one side, at about its mid-length where a large flap was formed stretching across almost to the mid-line. On the other side, slightly proximal to this level, a small cusp was present. Toward the distal end, there were two further lateral cusps, with the one on the same side as the flap tending to be more marked than the other. The distal end of the bract was pointed. Close to the tip, the dorsal surface was thickened into an oval patch of cells that surround and were interspersed with over 200 nematocysts, measuring c.  $63 \times 25 \mu\text{m}$ . Another small patch of such cells was found on the dorsal surface of the bract, in the mid-line, and on a level with the lateral flap. That patch, at least, is believed to be a site of bioluminescence. Proximally, the bracteal canal originated on the dorsal surface of the bract. It then curved over onto the ventral surface and continued distally in the mid-line. It appeared to be of variable thickness, but such variability was the result of variations in the thickness of the striated tissue that lay on each side of it. Close to the distal end of the bract the canal penetrated into the mesogloea and ended below the oval patch of epidermal cells.

The second type of bract (Fig. 10C, D) was similar to the first, but tended to be shorter, up to 20 mm in length, and broader. The lateral flap, however, was much reduced, although still an obvious feature. Distal to this again there was an obvious lateral cusp; but on the other side the cusp was very small or absent altogether. The first type of bract was about three times more numerous than the second. Roughly, with over a thousand bracts and approximately 25 gastrozooids, there would seem to have been about 40 bracts per cormidium. Very young bracts (Fig. 10E) were roughly pyramidal in shape with the distinctive patch of epidermal cells, including nematocysts, fully developed. The bracteal canal was short and did not extend onto the dorsal surface; while beneath the distal patch of epidermal cells it formed an extensive cavity.

**GASTROZOID.** (Fig. 11A, B). The gastrozooids measured up to c. 15 mm in length. The proboscis region, which often was curled back over itself, bore some stripes of gastrodermal cells. The stomach region, externally, was featureless and had a brown colour. The basigaster was greatly expanded on all sides, except that to which the tentacle was attached, and there was no obvious pedicle.

**TENTACLE AND TENTILLUM.** (Fig. 12). Typically the annulated tentacle had a muscular lamella running down one side, with the tentilla attached on the other side, at the internodes. The tentilla were of an extraordinary design. Only in the very young tentilla (Fig. 12 – centre) was there any trace of a pedicle. In these the cnidoband was made up of a large saccus overlain by a horseshoe-shaped band of nematocysts. The terminal process actually arose from the base of the saccus and bore, towards its distal end, a pair of ‘ocelli’. The gastrovascular canal penetrated through the terminal process, but no connection with the saccus of the cnidoband could be discerned. As the tentilla matured the cnidoband lengthened, with the terminal process still only attached close to its base. The saccus diminished in importance and distally the band of nematocyst occupied all but a narrow strip of the external surface of the cnidoband. Proximally, where the terminal process was attached, the band of nematocysts split into two parts on either side of the saccus. Three types of nematocysts were present. The large anisorhizas, which measured c.  $128 \times 27 \mu\text{m}$ , were arranged along the lateral margins of the cnidoband. Between them were numerous smaller nematocysts of two shapes, probably heteronemes, with the more cylindrical ones measuring c.  $40 \times 15 \mu\text{m}$  and the more ovoid ones c.  $32 \times 18 \mu\text{m}$ . Bands of musculature were present in the terminal process and extended distally to beneath the ‘ocelli’. In life this process was reddish-brown in colour.

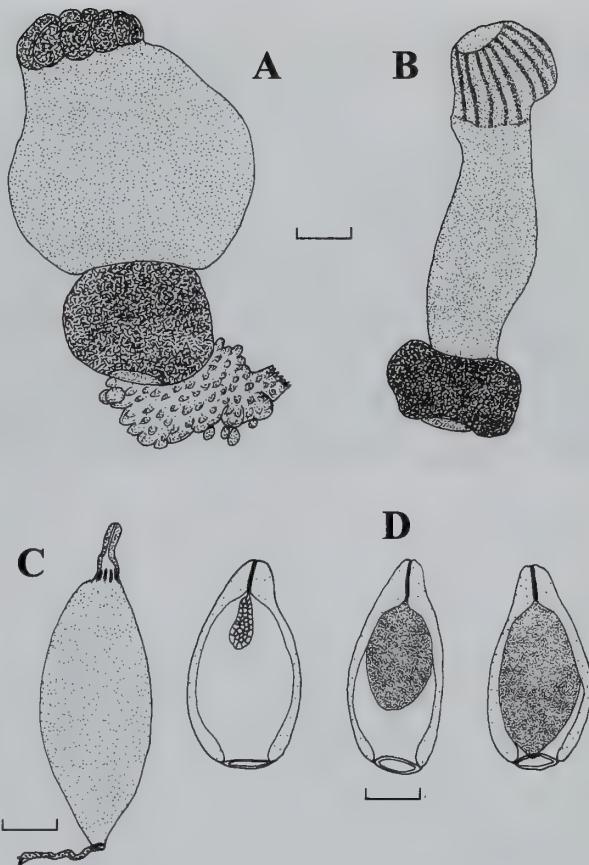


Fig. 11 *Erenna laciniata*. A., B. gastrozooids; C. palpon. Scale 2 mm. D. male gonophores. Scale 1 mm.

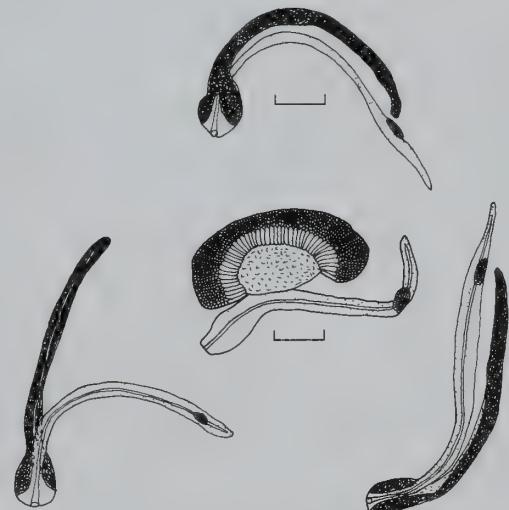


Fig. 12 *Erenna laciniata*. Three mature tentilla (Scale 1 mm), with (centrally) an immature one (Scale 0.5 mm).

**PALPON.** (Fig. 11C). Numerous palpons, up to c. 15 mm long, were present with the specimens. They were featureless thin-walled sacs filled, with a milky-white amorphous substance, although in life they were suffused with a brownish hue. The extent of the proboscis was variable, but typically, at its base, there were some



**Fig. 13** *Erenna laciniata*. Photograph of part of siphosome showing male gonophores.

short, brown-coloured stripes. No nematocysts were found on the palpacle.

**GONODENDRA.** (Figs 11D, 13). The JSL 1688 specimen was female and the gonodendra were arranged in a very similar fashion to that described in *Erenna richardi*. The JSL 1454 specimen was male, with the individual gonophores apparently scattered randomly down the stem (Fig. 13). Each was a relatively large medusoid, whose manubrium progressively filled with spermatozoa until it occupied almost the entire subumbrella cavity (Fig. 11D) and had a milky-white colour.

**DISTRIBUTION.** The JSL II Dive 1454 specimen came from the region of the Dry Tortugas between Florida and Cuba, while the Dive 1688 specimen came from the region of The Bahamas. In addition, some damaged nectophores that can be referred to this species have been found in the *Discovery* collections from individual hauls on the equator at 22°W (805–900 m) and at 3°N 23°W (0–1000 m).

**BEHAVIOUR.** In life the terminal process of the tentillum was reddish-brown in colour. It was kept rigid and was vibrated rapidly presumably, as was suggested for *Erenna richardi*, as a form of aggressive mimicry.

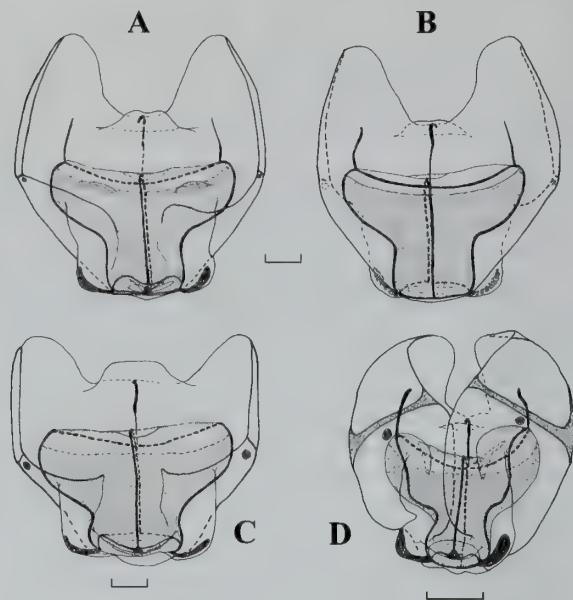
**ETYMOLOGY.** The specific name, being Latin for a ‘flap’, refers to the lateral flap-like process on the bracts.

#### *Erenna cornuta* sp.nov.

**HOLOTYPE.** The JSL II Dive 1451 specimen is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1818.

**MATERIAL EXAMINED.** The description is based on a single specimen collected during JSL II Dive 1451 at a depth of 896 m. (29 viii 1987; 24°30.6'N 83°45.6'W). In addition, a few specimens that apparently can be referred to this species have been found in recent *Discovery* collections, but always in a poor state of preservation.

**DIAGNOSIS.** Nectophores relatively less dorso-ventrally flattened, with only the basic ridge pattern; with apico-laterals not dividing close to ostium. Thrust block small, with no median indentation or conical protuberances. Lateral radial canals typically have ‘horn’ canals branching off at apico-lateral margins of nectosac. Bracts



**Fig. 14** *Erenna cornuta*. **A**, upper and **B**, lower views of nectophore with ‘horn’ canals; **C**, upper view of nectophore without ‘horn’ canals. **D**, upper view of young nectophore. Scale 2 mm.

with weak transverse ridge. Tentilla of two characteristic types; one with a long pedicle and no terminal process, with nematocysts grouped into four circular processes; the other with shorter pedicle and a small vesicular terminal process; with nematocysts, on the long cnidoband, more or less separated into c. 17 bundles.

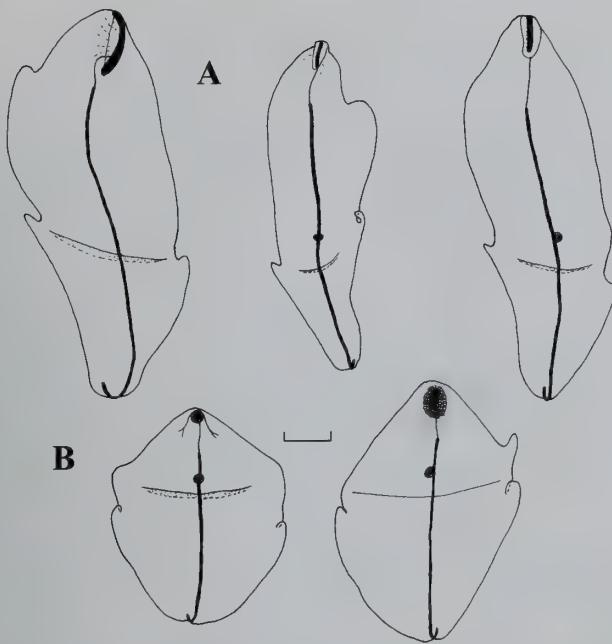
#### DESCRIPTION

**PNEUMATOPHORE.** Measured c. 1.5 × 1 mm, but its base has been ruptured by gas expansion. No obvious pigmentation.

**NECTOPHORE.** (Fig. 14). Thirteen large nectophores, plus two developing ones and some nectophoral buds, were found with the specimen. They measured up to 16 mm in length, 14 mm in width and 4 mm in depth. The ridge pattern comprised pairs of apico-, infra- and vertical laterals. The apico- and infra-laterals unite close to the apices of the axial wings. The infra-laterals extended basally to end below the ostium. The apico-laterals, on mature nectophores, were only prominent in the upper half of the nectophore and, unlike the two species described above, basal to the vertical lateral ridges, they curved in toward the mid line (Fig. 14A, C). They could be traced, usually only after staining, down further toward the ostium, but did not divide. On the youngest nectophore the apico-laterals rapidly approached and then overlapped each other, ending just above ostial level (Fig. 14D).

No obvious mouth plate and the ostium opened basally. On each side of the ostium there were prominent lateral processes with obvious strips of epidermal cells; with a smaller triangular patch of cells found dorsally. In addition, there was a pair of small patches of cells on either side of the nectophore; above the mid-height of and basal to the vertical lateral ridges. All these patches were believed to be sites of bioluminescence.

T-shaped nectosac with a distinct apical muscle-free area, particularly on its ventral side. Pallial canal short, extending from the base of the thrust block over on to the ventral surface of the nectophore, where it gave rise to the pedicular canal. On the nectosac the latter immediately divided to form the four straight radial canals. No pigmentation was noted in any canals. The lateral



**Fig. 15** *Erenna cornuta*. A. Three bracts of first type; B. two bracts of second type. Scale 2 mm.

radial canals passed through the middle of the muscle-free zone to reach the apex of the nectosac just short of its lateral margins. At that point the narrow 'horn' canals may or may not be given off. When present these 'horn' canals extended up for a variable distance, toward the apex of the nectophores, typically terminating on a level with the central thrust block. Eight nectophores (Fig. 14A, B) had well-developed 'horns', as did the two immature ones (Fig. 14D). In three others the 'horn' canals were ill-defined and short; while in the remaining two (Fig. 14C) there was no trace of them whatsoever.

The mature nectophores varied slightly in shape apparently in association with the extent of the 'horn' canals. The tapering axial wings were more extensive on those with well developed 'horn' canals; while the central thrust block typically was slightly smaller than those without 'horn' canals. The ones with ill-defined 'horn' canals tended to be intermediate. Of the 23 damaged nectophores collected at Discovery St. 7856#54 the 'horn' canals were prominent in all but the two smallest, but mature ones. The others were larger than the JSL II Dive 1451 ones, measuring c. 20 mm in length and width, and had denser musculature on the nectosac. The 'horn' canals also were more extensive, and there were traces of orange-

brown pigment in the basal parts of the radial canals and, particularly, the ostial ring canal.

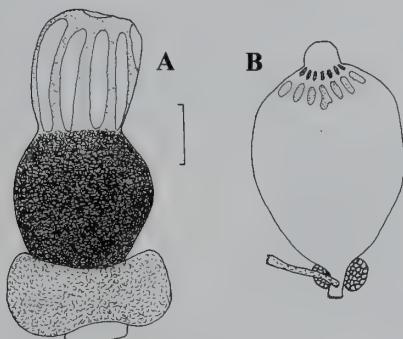
**BRACTS.** (Fig. 15). Two types of bract were present; the first (Fig. 15A), and considerably more numerous, being longer, up to 16 mm in length, and narrower than the second (Fig. 15B), which was up to 10 mm in length. Both types possessed a pair of lateral cusps. In the first type, as was the case with *Erenna richardi*, these seemed to lie at a fixed distance from the proximal end of the bract, and were asymmetrically disposed. Along the axis between these two cusps, on the dorsal surface of the bract, there was a rounded transverse ridge or process, that marked a change in the thickness of the bract, which was thinner distally. This ridge did not connect with the cusps, and its extent and distinctiveness was variable. Just distal to the ridge, in the mid-line, there was a small patch of cells; although often these have been abraded away.

On the second type of bract the lateral cusps were positioned, almost symmetrically, at about the mid-length of the bract. Just distal to these cusps there was a more or less pronounced cross-ridge which again demarcated a change in the thickness of the bract. Again a small patch of cells was situated distal to this ridge, in the mid-line. On the distal half of both types of bract, there could be an additional lateral protuberance of variable shape. At the distal tip of both types the dorsal surface was raised up in the mid-line to form an elongate or elliptical process on which were found a concentration of small epidermal cells, with brownish-red pigment. Centrally, these cells included some nematocysts, which measured c. 68 × 32 µm.

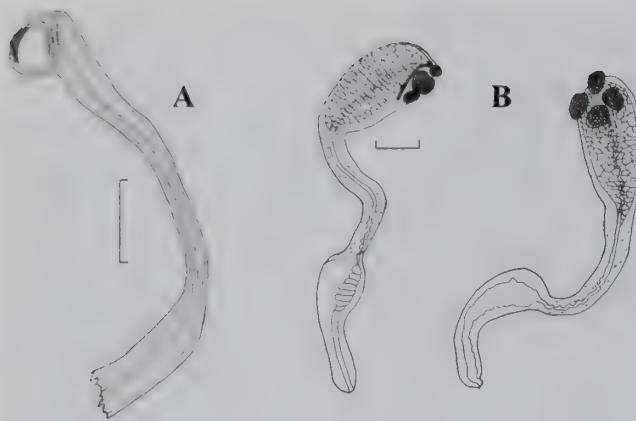
The bracteal canal originated, proximally, slightly over on the dorsal surface of the bract. It passed down the middle of the bract in close contact with its ventral wall, with striated bands of cells lying on either side of it, indicating where the muscular lamella was attached. At some distance from the distal end of the bract, in comparison with *Erenna richardi*, the canal penetrated into the mesogloea and curved up to end beneath the proximal part of the concentration of cells on the dorsal surface.

**GASTROZOOID.** (Fig. 16A). Only three well-developed gastrozooids remained with the specimen. The largest was 6 mm in length. The basigaster formed a horseshoe-shaped, laterally expanded structure around the base of the gastrozoid, with the tentacle attached in the open zone. It was a light brown colour. No obvious pedicle. The expanded stomach was externally featureless and had a dark brown colour. The proboscis region, which was about the same length as the stomach, had distinct stripes.

**TENTACLE AND TENTILLUM.** (Figs 17, 18). The tentacle was annulated, with a muscular lamella running down one side, and the tentilla attached, on the opposite side, at the internodes. There were two types of tentilla, both of which were found attached to the same tentacle. Early on in the development of the first type (Fig. 17A), the tentillum consisted of a long pedicle and a minute cnidoband devoid of nematocysts. The gastrovascular canal was seen, at the end of the pedicle, to turn back and continue down to open into the cavity of the saccus of the cnidoband. With further development the connection with the saccus cavity was closed, and the cavity filled with gastrodermal cells. A remnant of the diverticular canal seemed to persist, passing through a relatively dense band of gastrodermal cells. In the mature tentillum (Fig. 17B), the proximal part of the pedicle was expanded, typically tapering towards its base. The gastrovascular canal could occupy most of the interior, or could remain as a narrow tube, which became twisted and folded up on one side of the pedicle. Distally the pedicle was narrower, with the canal often having a zigzag appearance, probably indicating some



**Fig. 16** *Erenna cornuta*. A. gastrozoid, and B. palpon. Scale 1 mm.



**Fig. 17** *Erenna cornuta*. A. young tentillum of first type. Scale 0.5 mm.  
B. Two views of mature tentillum of first type. Scale 1 mm.

contraction in the length of the pedicle itself. The canal penetrated through the saccus of the cnidoband to its tip. The saccus was largely filled by large, vacuolate gastrodermal cells that formed a reticulate pattern. The nematocysts were restricted to four circular swellings; two lateral, one proximal, one distal. Three types of nematocysts were present and arranged so that the larger anisorhizas, measuring c.  $130 \times 35 \mu\text{m}$ , surrounded the smaller (?) haplonemes; the more cylindrical ones measuring  $32 \times 11 \mu\text{m}$ , and the more ovoid ones  $41 \times 14 \mu\text{m}$ .

The youngest of the other type of tentillum (Fig. 18A) comprised a short, thickened pedicle, a long cnidoband, and a short terminal process, which had a circular spot of distinctive epidermal cells on one side. The broad gastrovascular canal was present throughout and, in the terminal process, it appeared to bend back and continue, for a short distance, toward the saccus of the cnidoband. However, even in the smallest tentilla examined, the saccus had already been occluded by gastrodermal cells. The nematocysts had begun to accumulate into an undulating series of connected swellings on one side of the saccus.

Only a few mature tentilla (Fig. 18B) of the second type were found with the specimen. In these the pedicle remained short and broad and was largely filled by the gastrovascular canal. The cnidoband had increased greatly in length and was largely filled by

large, vacuolated gastrodermal cells. The narrow gastrovascular canal passed through its middle and opened into the cavity of the small, spherical, thin-walled terminal process. The patch of cells persisted on one side of the latter. No diverticular branch of the main canal could be discerned. On the cnidoband the rounded swellings containing the nematocysts became more or less separated one from another. On the two best preserved mature tentilla there were 17 of these patches. The nematocysts were of the same type and size as on the other type of tentillum.

**PALPON.** (Fig. 16B). The globular, thin-walled palpons measured up to c. 4 mm in length. There was a short, narrow proboscis, at the base of which was a ring of pigmented gastrodermal cells, often organised into distinct spots. Other concentrations of gastrodermal cells sometimes were visible, particularly on the distal part of the stomach region. The base of the stomach region was almost surrounded by a small, loosely attached, horseshoe-shaped region of large, vacuolated epidermal cells, with the palpacle being attached in the open region. No nematocysts were found on the palpacle.

**GONODENDRON.** No gonodendra were found on the small piece of siphosome that remained with the specimen.

**DISTRIBUTION.** The type specimen came from the region of the Dry Tortugas, between Florida and Cuba. Nectophores with 'horn' canals, which presumably can be referred to this species, have been collected at four recent *Discovery* stations. Two of these were at c.  $30^\circ\text{N}$   $23^\circ\text{W}$  at depths of 1250–1500 m and 1500–2000 m, and the other two from off Bermuda (c.  $31^\circ 45'\text{N}$   $63^\circ 45'\text{W}$ ) at depths of 1250–1500 m.

**ETYMOLOGY.** The specific name, meaning 'horned' in Latin, refers to the 'horn' canals present in most of the nectophores.

### *Parerenna* gen. nov.

**DIAGNOSIS.** Nectophores not dorso-ventrally compressed; with muscle-free zone on nectosac mainly on lower surface adaxially. Vertical lateral and incomplete infra-lateral ridges very indistinct; the latter not forming the lower margin of lateral surface. Apico-laterals peter out well above ostial level. Gastrozooid with minute basigaster. Tentillum with long pedicle; with cnidoband extending beyond terminal process, which has a small spherical distal swelling.

Monotypic genus to accommodate *Parerenna emilyae* sp.nov.

### *Parerenna emilyae* sp.nov.

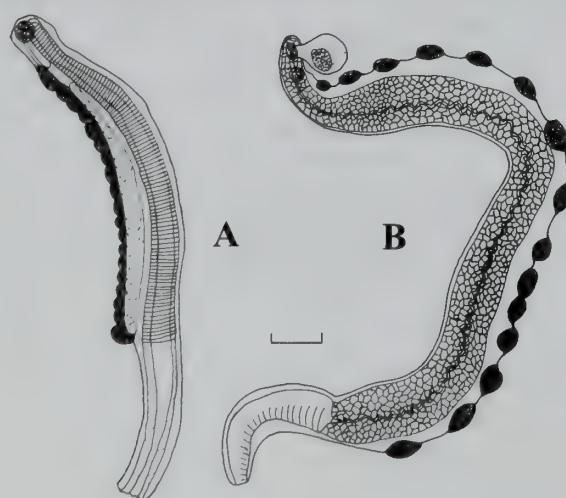
**HOLOTYPE.** The specimen from JSL I Dive 2886 is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1820.

**MATERIAL EXAMINED.** A single specimen collected during JSL I Dive 2886 (18 xii 1990;  $26^\circ 31.8'\text{N}$ ,  $78^\circ 05.6'\text{W}$ ; depth 823 m). Before preservation in 5% buffered formalin, the bioluminescence of the specimen was studied which, unfortunately, resulted in the loss of some parts.

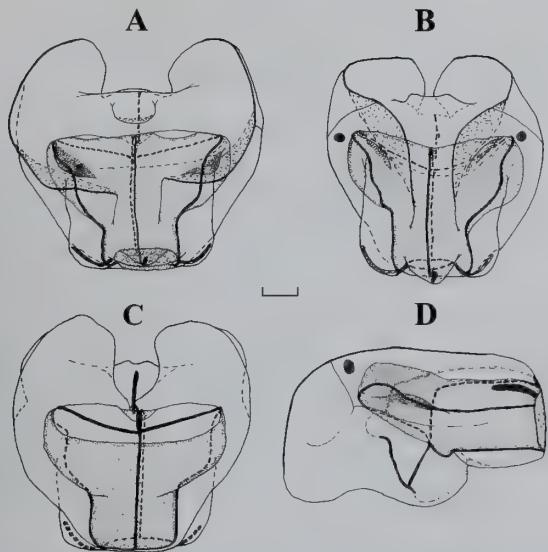
**DIAGNOSIS.** As for genus.

### DESCRIPTION

**PNEUMATOPHORE.** The base of the pneumatophore has exploded due to the expansion of the gas contents while bringing the specimen to the surface. Pneumatosaccus spherical, c. 1 mm in diameter, with a small cap of cells, which may have been pigmented in life.



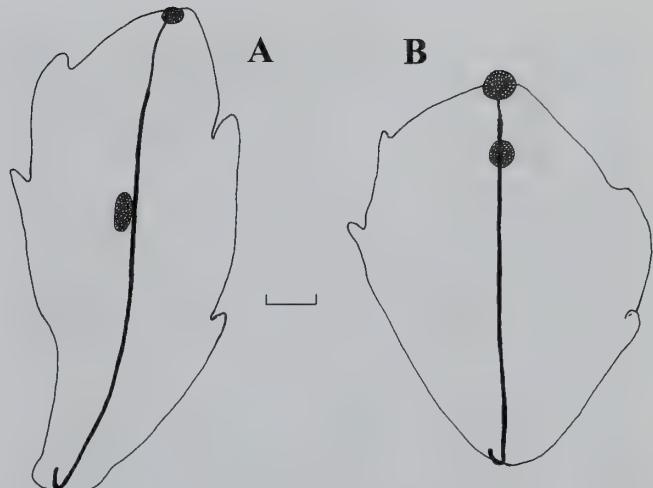
**Fig. 18** *Erenna cornuta*. A. Young tentillum of second type. Scale 0.5 mm.  
B. Mature tentillum of second type. Scale 1 mm.



**Fig. 19** *Parerenna emilyae*. Nectophores. A., B. upper, C. lower, and D. lateral views. Scale 2 mm.

**NECTOPHORE.** (Fig. 19). Eight fully developed and two developing nectophores were found with the specimen; plus a few nectophoral buds at the apex of the highly contracted nectosome. Mature nectophores were not dorso-ventrally flattened and measured up to 13 mm in length and width and 6 mm in height, and had well developed tapering axial wings. The central thrust block was broad, but of little height. The only obvious ridges were the apico-laterals (Fig. 19A, B), running down from the apices of the axial wings toward the ostium, but petering out well above that level. Only by staining were the pairs of complete vertical lateral and incomplete infra-lateral ridges revealed. The latter did not form the lower margins of the lateral surface of the nectophore (Fig. 19D). Two small patches of cells were found on each side of the nectophore, just basal to the vertical lateral ridges, although for many nectophores they had been abraded away. In addition there were three distinct strips of small epidermal cells, one dorsal and two lateral, stretching up from the ostium; the lateral pair being more extensive and pronounced than the dorsal one. These were all believed to be sites of bioluminescence. Mouth plate absent. Ostium opened basally.

The nectosac was Y-shaped in the younger nectophores, but the median apical indentation was less pronounced in the larger ones.

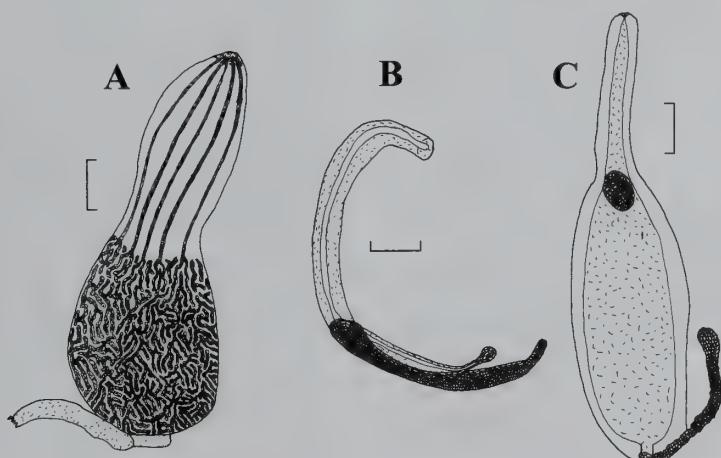


**Fig. 20** *Parerenna emilyae*. Bracts of A. the first and B. the second type. Scale 1 mm.

and may disappear altogether; the nectosac then being T-shaped. There was a large muscle-free zone on the apical, adaxial part of its lower side. The pallial canal was quite long, extending from the base of the thrust block to beyond the point of origin of the pedicular canal. The long pedicular canal was inserted onto the nectosac either at the point of origin of the lateral radial canals, or slightly basal to it. On half of the fully developed nectophores there was a slight asymmetry in the origin of the lateral radial canals with either the left or the right branching off before the other. The dorsal and ventral canals were straight and ran directly to the ostial ring canal. There was, however, a slight loop in the lateral radial canals as they curved over onto the lateral surface of the nectosac slightly above its mid-height. These canals then curved down to the mid-level and continued to the ostial ring canal.

**SIPHOSOME.** The remaining piece of siphosome was highly contracted, with four gastrozooids and four palpons still attached. There were no signs of any gonodendra.

**BRACTS.** (Fig. 20). Twenty-two bracts, up to 9 mm in length, remain with the specimen. Two basic types, present in approximately equal numbers, could be distinguished. The first (Fig. 20A) was longer, but narrower, than the second (Fig. 20B). Both types



**Fig. 21** *Parerenna emilyae*. A. Gastrozooid. Scale 1 mm. B. Tentillum and C. Palpon. Scales 0.5 mm.

have two pairs of lateral cusps; although in the shorter, more rounded bracts, one or both of the more distal pair could be difficult to discern. Both types had a patch of small epidermal cells on the dorsal surface, but the positioning differed (Fig. 20). Often these patches had been abraded away. Proximally the bracteal canal originated on the dorsal surface of the bract. It passed down the middle of the ventral side bract and, for the most part, lay in close contact with its surface. A short distance from its distal end it narrowed and penetrated through the mesogloea to terminate beneath a hemispherical clump of epidermal cells sunk into the mesogloea. Some of these cells, as with the patches on the dorsal surface of the bract, probably produced bioluminescence; others were nematocysts measuring  $80 \times 20 \mu\text{m}$ .

**GASTROZOOID.** (Fig. 21A). Up to 7.5 mm long, with no obvious pedicle. The basigaster, to which the tentacle was attached, was minute. The gastrodermal lining of stomach region bore a complex pattern of villi; while the proboscis was broad and elongate, with a distinctive arrangement of eight stripes.

**TENTILLUM.** (Fig. 21B). The tentillum was very distinctive, with a thickened pedicle, occupying about half its length, through which the broad gastrovascular canal passed. The distal half of the tentillum consisted of an extensive cnidoband and a process, containing a canal, that bent away, occasionally at a right-angle, from the base of the cnidoband and was terminated by a small spherical swelling. The cnidoband appeared to have two rows of large nematocysts on either side, measuring  $120 \times 20 \mu\text{m}$ , that, judging by those that had been discharged, probably were homotrichous anisorhizas. The remainder of the cnidoband bore numerous smaller nematocysts of two sizes; the more cylindrical ones measuring c.  $21 \times 12 \mu\text{m}$ , and the more ovoid ones c.  $26 \times 15 \mu\text{m}$ . These were the only nematocysts to be found on the distal tip of the cnidoband.

**PALPON.** (Fig. 21C). Up to 4 mm long, with a palpacle, without nematocysts, at its base. Proboscis region long and narrow with broad gastrovascular canal.

**DISTRIBUTION.** Known only from a single specimen collected in the region of The Bahamas.

**REMARKS.** Although *Parerenna emilyae* possesses the general erennid characters, there are certain differences from those of the genus *Erenna* that warrant its placement in a separate genus. Primarily, the nectophores are not flattened dorso-ventrally and only the apico-lateral ridges are distinct. The weak infra-lateral ridges do not demarcate the lower margins of the lateral facets, and the weak vertical lateral ridges have an oblique course. Further, the lateral radial canals on the nectosac are slightly curved. In addition the basigaster of the gastrozooid is minute, especially in comparison with the greatly expanded basigasters of the *Erenna* species.

**ETYMOLOGY.** The species is named for my daughter Emily.

## KEY FOR THE IDENTIFICATION OF ERENNID NECTOPHORES

- 1 Nectophores dorso-ventrally flattened with distinct, short vertical lateral ridges, and apico- and infra-lateral ridges joining apically. Genus *Erenna* ..... 2  
 Nectophores not dorso-ventrally flattened; indistinct vertical lateral ridges; indistinct infra-lateral ridges not joining apico-laterals apically. Genus *Parerenna* ..... *P. emilyae*

- 2 Two digitate processes on ventral side of thrust block .....  
*Erenna richardi*  
 No digitate processes on ventral side of thrust block ..... 3  
 3 Apico-lateral ridges divide close to ostium; thrust block with V-shaped median indentation; no 'horn' canals ..... *Erenna laciniata*  
 Apico-lateral ridges do not divide close to ostium; thrust block without median indentation; 'horn' canals usually present ..... *Erenna cornuta*

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XX(340060.1)

# A new species of loach, genus *Nemacheilus* (Osteichthyes, Balitoridae) from Aceh, Sumatra, Indonesia

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**SYNOPSIS.** A new species of the balitorid genus *Nemacheilus* is described from Aceh, Sumatra. The new species is distinguished from other *Nemacheilus* species by the combination of a colour pattern of dorsal saddles and lateral blotches but without a dark spot at the anterior base of the dorsal fin and the presence a row of enlarged, elongate, posteriorly directed, teardrop shaped scales on either side of the lateral line scale row on the anterior part of the caudal peduncle, each of which bears a comparatively large, retrorse, apical tubercle.

## INTRODUCTION

Little has been reported about fishes inhabiting inland waters of Aceh, Sumatra (Kreemer, 1922 (*fide* Wirjoatmodjo, 1987); Fowler, 1940; Wirjoatmodjo, 1987; Hadiaty and Siebert, 1998). A small collection of fishes was made from Sungai Lembang, Gunung Leuser National Park-Aceh Selatan during August–September 1997, as part of an ecosystem mapping project from the Research and Development Centre for Biology, Bogor. Gunung Leuser National Park, established in 1980, comprises 792,675 hectares of prime habitat. It, and an associated management area, include coastal lowlands, uplands, and montane habitats. The area is home to tiger, elephant, rhinoceros, orangutan and spectacular plants such as *Rafflesia atjehensis* and *Amorphophalus* sp. The fish collection contains several distinctive fishes, of which two species of *Osteochilus* were described earlier (Hadiaty & Siebert, 1998). The collection also contains a new species of the balitorid sub-family Nemacheilinae that has enlarged and elongate scales bordering the lateral line in anterior half of the caudal peduncle, each of which bears a large, retrorse tubercle near its posterior tip.

The Indonesian and Malaysian nemacheiline loaches were last revised by Kottelat (1984), who recognised nine species in the region but noted that several nominal taxa, especially some from Sumatra, could not be critically evaluated because of the lack of sufficient material. Since then Chin and Samat (1992) have described *N. elegantissimus* from Sabah, Malaysia and Kottelat *et al.* (1993) have recognised as valid two of the species, *N. pfeifferae* and *N. longipinnis*, that Kottelat could not evaluate earlier. The number of valid species recognised species in the region now stands at 12. Two of the species in the area, *N. selangoricus* and *N. spiniferus*, have acuminate scales, each of which bears a large tubercle, along the lateral line on the caudal peduncle. One, *N. selangoricus*, is widely distributed, occurring in Sumatra, Malaysia, and Borneo, while the other, *N. spiniferus*, is known only from Borneo (Kottelat *et al.*, 1993).

specimens of the new species were collected by electrofishing and are deposited at the Museum Zoologicum Bogoriense (MZB), Research and Development Centre for Biology, Cibinong, Java, Indonesia and The Natural History Museum (BMNH), London. The egg count was done by direct enumeration. Illustrations of scales and mouthparts were rendered from camera lucida tracings. Statistical testing of differences in the shape of caudal peduncle scales between males and females of the new species and between the new species and *N. chrysolaimos* are based on measurements of camera lucida tracing of individual scales made under compound microscopy. The abbreviation ZMA is for Zoologisch Museum, Amsterdam. Peter Bartsch, Museum fuer Naturkunde der Humboldt-Universitaet zu Berlin, examined the holotypes of *N. dunckeri* (ZMB 20546) and *N. longipinnis* (ZMB 20547) for us; he also provided a translation of Ahl's (1922) description of the colour pattern of each species.

## SYSTEMATICS

### *Nemacheilus tuberigum* sp.nov.

(Figs. 1–5; Tables 1, 2)

Holotype, MZB 9356 (48.5 mm SL, 59.2 mm TL); Indonesia, Sumatra, Aceh Selatan, Kecamatan Klut Selatan, Desa Pucuk Lembang, Gunung Leuser National Park, caught in a clear forest stream tributary to Sungai Lembang; R.K. Hadiaty and A. Mun'im, 2 September 1997.

Allotype, MZB 10565 (43.0 mm SL); same data as holotype.

Paratypes, MZB 9357, 12 ex., (39.6–53.2 mm SL); same data as holotype. BMNH 2000.4.10.1–5, 5 ex., (42.2–50.5 mm SL); same data as holotype. MZB 9358, 4 ex., (44.8–53.4 mm SL); same location as holotype; R.K. Hadiaty and A. Mun'im, 31 August 1997. MZB 9359, 1 ex., (42.6 mm SL); same location as holotype; R.K. Hadiaty and A. Mun'im, 1 September 1997. MZB 9360, 4 ex., (42.6–49.2 mm SL) Indonesia, Sumatra, Aceh Selatan, Desa Pucuk Lembang, Alur Betung, a tributary of S. Lembang; R.K. Hadiaty and A. Mun'im, 2 September 1997. MZB 9361, 2 ex., (31.9 and 37.2 mm SL); Indonesia, Sumatra, Aceh Selatan, Suag Balimbing Research

## MATERIALS AND METHODS

Methods for counts and measurements follow Kottelat (1984). The



**Fig. 1** A. Holotype of *N. tuberigum*, MZB 9356, 48.5 mm SL, gravid female. B. Allotype of *N. tuberigum*, MZB 10565, 43.0 mm SL, mature male. Scale bar in mm.

Station, caught in a muddy forest stream tributary to Sungai Lembang; R.K. Hadiaty and A. Mun'im; 4 September 1997.

Non-type materials: MZB 9351, 10 ex., (38.0–53.0 mm SL); data as for holotype. MZB 9362, 28 ex., (33.2–45.9 mm SL); location as for holotype; R.K. Hadiaty and A. Mun'im; 31 August 1997. MZB 9363, 27 ex., (34.7–52.2 mm SL); location as for holotype; R.K. Hadiaty and A. Mun'im; 1 September 1997. MZB 9364, 11 ex., (33.2–52.3 mm SL); Indonesia, Sumatra, Aceh Selatan, Desa Pucuk Lembang, Alur Betung, a tributary of Sungai Lembang; R.K. Hadiaty and A. Mun'im; 2 September 1997. MZB 10566, 2 ex., (47.2–48.2 mm SL); unnamed tributary of S. Alas, behind the camp at Ketambe Research Station, Aceh, Sumatra, Indonesia; R.K. Hadiaty & A. Mun'im; 21 June 1998. MZB 10567, 3 ex., (38.6–52.9 mm SL); unnamed tributary of S. Alas, Ketambe Research Station, Aceh,

Sumatra, Indonesia; R.K. Hadiaty & A. Mun'im; 20 June 1998. MZB 10568, 5 ex., (41.2–52.8 mm SL); unnamed tributary of S. Alas, in front of the National Park camp ground, Ketambe, Aceh, Sumatra, Indonesia; R.K. Hadiaty & A. Mun'im; 23 June 1998. MZB 10569, 2 ex., (39.8–44.9 mm SL); mouth of S. Sukarimbun, Ketambe, Aceh, Sumatra, Indonesia; R.K. Hadiaty & A. Mun'im; 20 June 1998. MZB 10570, 15 ex., (28.2–59.6 mm SL), unnamed tributary of S. Alas, behind the camp of the Ketambe Research Station, Sumatra, Indonesia; R.K. Hadiaty & A. Mun'im; 21 June 1998.

**DIAGNOSIS.** *Nemacheilus tuberigum* is easily distinguished from all other *Nemacheilus* by the following combination of characters: a row of comparatively large tubercles present on enlarged, elongate scales in the scale rows immediately above and below the lateral line scale row on the anterior half of the caudal peduncle, (comparatively large tubercles in a similar position present also in *N. selangoricus* and *N. spiniferus*, but on scales with peculiar posterior elongate processes); and colour pattern consisting of 11–15 dorsal saddles, a series of 8–13 lateral blotches centered along the lateral line and without a dark spot at anterior base of dorsal fin (present in *N. selangoricus* and *N. spiniferus*).

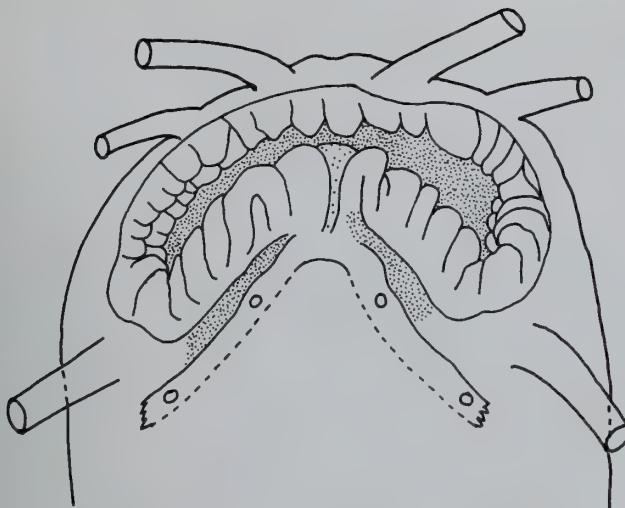
**DESCRIPTION.** General appearance and physiognomy are shown in Figure 1; morphometric and meristic data for the holotype and paratypes (range, as the minimum and maximum observation, mean and standard deviation) are given in Table 1. *Nemacheilus tuberigum* presents a shape and colour pattern general for many members of the genus.

Dorsal head length 5–6 times in SL; eye moderate, shorter than snout, 3–4 times in dorsal head length; suborbital flaplet present in males at anteroventral corner of eye, anterior nares a short tube (Fig. 2); small tubercles scattered over dorsal and lateral exposures of the head. Cephalic lateral line pores: supraorbital canal with 5 pores; post-temporal canal with 3 pores, infraorbital canal with 10 pores, supracapillary canal with 3 pores; operculomandibular canal with 9 pores.

Mouth crescent-shaped (Fig. 3), with three pairs of barbels: anterior rostral barbel shortest, reaching to about middle of eye; posterior rostral barbel longest, reaching to half way between hind edge of eye and hind edge of opercle; mandibular barbel intermediate



**Fig. 2** Lateral view of the head of the allotype of *N. tuberigum*, MZB 10565. Suborbital flap clearly evident; anterior naris a short tube, valve-like; small tubercles are scattered over the head.

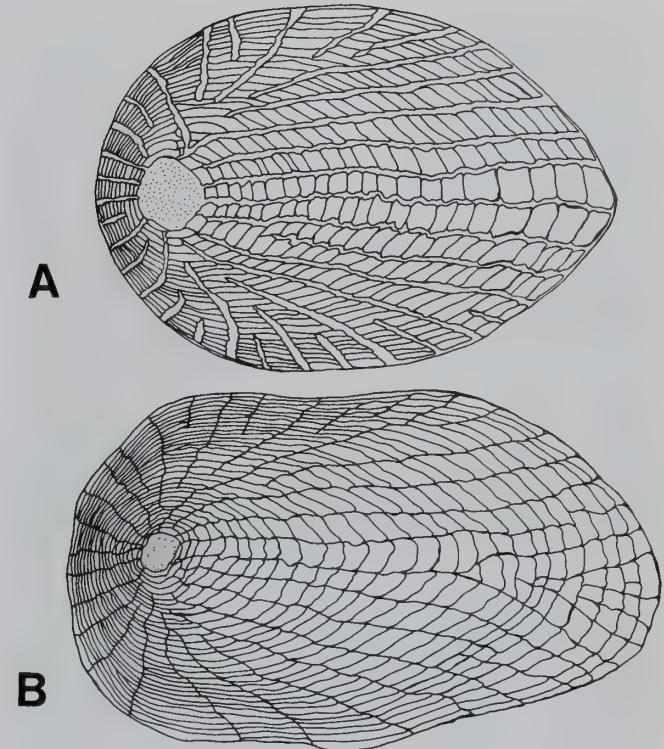


**Fig. 3** Mouth of *N. tuberigum* MZB 9357, male, 48.4 mm SL. Lower lip completely separated at the midline; upper lip weakly crenulate, weakly papillate in posterolateral part.

in length between rostral barbels, reaching to end of posterior rostral barbel (Fig. 2). Process dentiformis small. Lips moderately fleshy: upper lip weakly crenulate to feebly papillose, posterolateral parts of upper lip weakly papillose; lower lip with a median incision completely separating right and left sides, with 2 or 3 deep pleats on either side of median incision.

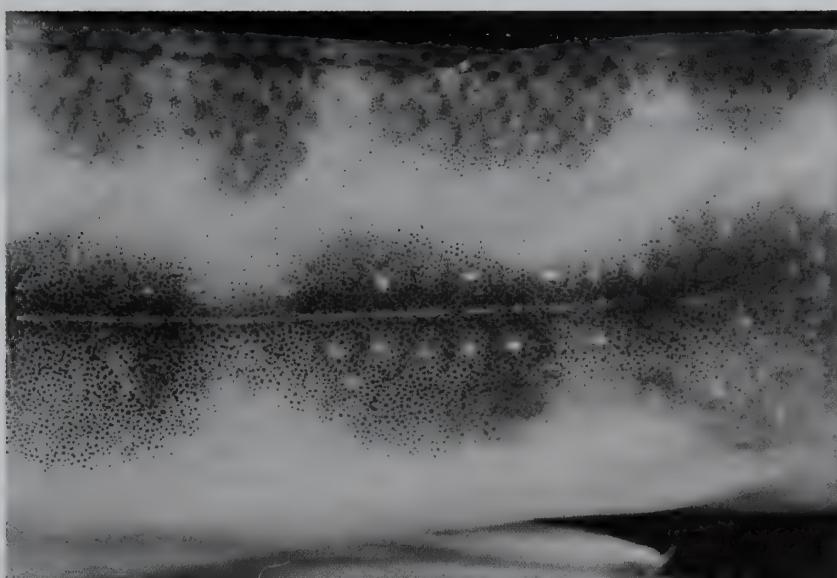
Pectoral fin with 11 rays, reaching at most only halfway to pelvics; pelvics with 8 rays, nearly reaching anus, anal fin not reaching caudal fin. Hindborder of pectoral and pelvic fins with prolongations at extremities of rays. Caudal fin forked, short.

Body fully scaled scales small, ovoid slightly pointed posteriorly. Scales on caudal peduncle larger and longer than those from mid-body region. Scale rows immediately above and below the lateral line on the anterior part of the caudal peduncle with 5–10 obviously



**Fig. 4** Scales of *N. tuberigum*. A. Scale from mid-body below dorsal fin. B. Scale from scale row immediately adjacent to lateral line on caudal peduncle. These scales usually bear an enlarged tubercle near the posterior margin. Anterior to the left; scale bar = 0.1 mm.

elongate scales (Fig. 4) ( $l/w$  for males  $\bar{x} = 1.64$ , s.d. = 0.055,  $n = 5$ ;  $l/w$  for females  $\bar{x} = 1.55$ , s.d. = 0.097,  $n = 5$ ), usually tear-drop in shape, each bearing a large retrorse tubercle (Fig. 5) as on the acuminate scales of *N. selangoricus* and *N. spiniferus*.



**Fig. 5** Close up of anterior caudal peduncle of allotype of *N. tuberigum* (anterior to the left). Lateral line passes through the upper third of the three oval lateral blotches; small tubercles are scattered over the caudal peduncle generally. A row of larger tubercles can be seen on either side of the lateral line, beginning near the left edge of the second lateral blotch and ending near the left edge of the third blotch.

Lateral line complete, with 76–90 pores, incomplete in specimens less than about 30 mm SL.

In alcohol body pale yellowish with 10–15 irregular dorsal saddles, saddles wider than saddle interspaces. There are 8–13 blotches along the lateral line, blotches progressively larger posteriorly (Fig. 1b). In larger specimens blotches may be fused to form longitudinal stripe, especially in posterior half of body (9 of 29 specimens with such a longitudinal stripe). No spot present at anterior base of dorsal fin. Two dark marks at base of caudal-fin rays: the larger, more intense mark a vertically elongate dark mark in series with lateral blotches; the smaller, a dorsally situated, oval, dark spot, perhaps in series with dorsal saddles.

**SEXUAL DIMORPHISM.** In our material, the largest individuals are female: no male exceeded 48.5 mm SL while several females exceeded this length, the longest of which is 53.4 mm SL. Males (39.8 mm SL and over) possess a large subocular flaplet (Fig. 2) below the anteroventral margin of eye and have a greater number of tubercles in the mid-body region than females. In males retrorse tubercles are present on each scale in the region between the pelvic fin and the lateral line, in well-defined rows. Tubercles are also present in females in this region, but they are scattered rather than present in rows on every scale; tubercles of females are also smaller than those of males. Above the lateral line in the mid-body region both sexes have tubercles variously scattered.

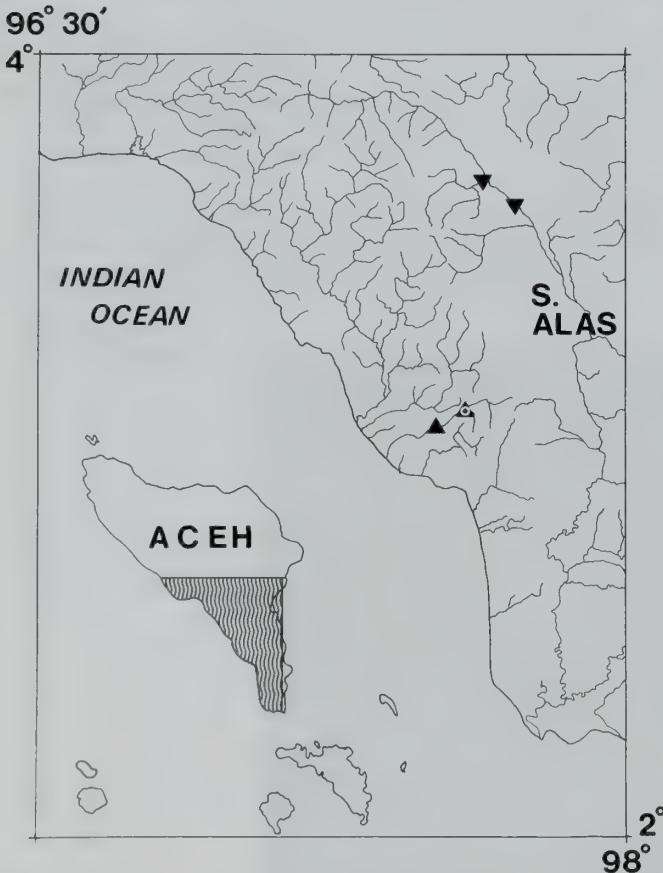


Fig. 6 Drainage map of Gunung Leuser National Park area from which *N. tuberigum* materials have been captured; the shaded area of the inset is the area covered by the drainage map. ▲ = S. Lembang localities near Suag Balimbing Research Station; target symbol = type locality. ▼ = S. Alas drainage localities near Ketambe Research Station.

**REPRODUCTION.** Yellow to orange mature eggs were visible through the thin abdominal skin of female with a distended belly. Another female, 48.5 mm TL, contained 4192 eggs of uniform size (0.61 mm mean diameter). Fishes that spawn all eggs in a single event are known as total spawners (Welcomme, 1979). One of the characteristics associated with total spawning is uniform egg size. Since eggs of *N. tuberigum* were observed to be of uniform size we interpret the species as most likely being a total spawner.

**DISTRIBUTION AND HABITAT.** *Nemacheilus tuberigum* is known only from Sungai Lembang, Suag Balimbing Research Station and Sungai Alas, Ketambe Research Station in the region of Gunung Leuser National Park, Aceh, Sumatra (Fig. 6). It was taken from streams of small to moderate size, mostly in shallow, clear water, but a few juveniles were taken from murky water. The substrate over which it was found varied from gravelly to sandy. Species co-occurring with *N. tuberigum* were: *Homaloptera rileyi*, *H. gymnogaster*, *Tor tictobra*, *Rasbora lateristriata*, *R. sumatrana*, *R. meinerti*, *Glyptothorax cf. major* and *G. cf. platypogonoides*. Given the lack of general information on fish distributions in Sumatra it would not be surprising to find the species elsewhere.

**ETYMOLOGY.** The epithet *tuberigum*, a noun, is derived as suggested in Brown (1956: p. 44). It is constructed in reference to the comparatively large tubercles on either side of the lateral line on the anterior part of the caudal peduncle; it is from the Latin words *tuber*, a neuter noun meaning swelling, and *mangus*, meaning large, the latter dismembered to *-gus*, but modified appropriately to the gender of *tuber*.

## COMPARISONS WITH OTHER SPECIES

**EXTERNAL CHARACTERS.** The presence of a row of enlarged tubercles on the caudal peduncle on the apex of elongated scales of the scale rows immediately above and below the lateral line scale row immediately separates *N. tuberigum* from all other known *Nemacheilus* except *N. selangoricus* and *N. spiniferus*. The lack of a dark spot at the anterior base of the dorsal fin immediately distinguishes *N. tuberigum* from these latter two taxa; additional differences from these two species are recorded in Table 2. Nevertheless it is worthwhile to consider some general comparisons with other *Nemacheilus* from Sumatra, which include (Kottelat *et al.*, 1993; Kottelat & Whitten, 1996) *N. fasciatus*, *N. kapuasensis*, *N. lactogeneus*, *N. longipinnis*, and *N. pfeifferae* and the possibly valid nominal taxa *N. dunckeri*, *N. papillosa* and *N. jaklesii*. A third party reviewer also requested a comparison to *N. masyae*, a species present in peninsular Thailand and Malaysia at about the same latitude as *N. tuberigum*.

**COLOUR PATTERN.** The colour pattern of *N. tuberigum* is a series of dorsal saddles and midlateral blotches, a colour pattern general for all Sumatra *Nemacheilus* of which we are aware except *N. lactogeneus*. Nevertheless, *N. tuberigum* is distinguishable from some of the other species of *Nemacheilus* from Sumatra in matters of colour pattern details.

*Nemacheilus fasciatus*, *N. jaklesii* and *N. longipinnis* each possess a dark spot at the anterior base of the dorsal fin, which *N. tuberigum* lacks. In addition, *N. jaklesii* appears to have a colour pattern of dorsal saddles nearly confluent with relatively deep vertical, lateral bands rather than blotches along the lateral line. The photograph of the type of *N. longipinnis* reproduced in Kottelat *et al.* (1993; Fig. 139) indicates a dark spot at the base of the anterior part

of the dorsal fin even if the colour pattern is not evident on the rest of the body. Peter Bartsch examined this specimen for us and confirms the presence of the spot, although now faded, which Ahl (1922) specifically mentions in the description of the colour pattern of the species. *Nemacheilus longipinnis* also seems to have a larger eye than *N. tuberigum*, in which the eye is noticeably shorter than the snout.

With 10–15 dorsal saddles and 8–13 lateral blotches, *N. tuberigum* has generally fewer dorsal saddles and lateral blotches than *N. pfeifferae* (10–18 dorsal saddles, 10–15 lateral blotches; data from Kottelat *et al.*, 1993), the photograph of which in Kottelat *et al.* also shows its lateral blotches fused into a more or less continuous band from the opercle to the base of the caudal fin. We have examined 2 syntypes of *N. papillosa*, the condition of which is not very good. However, traces of the colour pattern are still evident; the colour pattern seems to consist of dorsal saddles with a well defined, relatively narrow, lateral band 3 scale rows wide centered on the lateral line, at least on the posterior half of the body. Lateral blotches in *N. tuberigum* may become confluent to form a lateral band, especially in the posterior half of the body, but in our material it is never as narrow or as distinct as in the syntypes of *N. papillosa* we examined. The colour pattern of some populations of *N. kapuasensis* is readily distinguishable from that of *N. tuberigum*. Dorsal saddles and lateral blotches of these *N. kapuasensis* are equal in number and more or less confluent, rendering a appearance of dorsal saddles that extend ventrally to the level of the insertion of the pectoral fin (see Kottelat, 1984: Fig. 16b; Kottelat *et al.*, 1993: Pl. 25). Dorsal saddles and lateral blotches of *N. tuberigum* form two clearly separate series.

Kottelat *et al.* (1993) suggest *N. dunckeri* may be a synonym of *N. pfeifferae*. The holotype of *N. dunckeri* was examined for us by Peter Bartsch. He reports the specimen to be faded but that there is no indication of a dark spot at the anterior base of the dorsal fin; Ahl (1922) specifically stated there are no spots on any of the fins. Ahl also described a sharply defined dark lateral stripe, wider than eye diameter, extending from the opercle to the caudal peduncle. The lateral blotches of *N. tuberigum* do not form such a band, not even on the caudal peduncle of the largest specimens examined by us.

True *N. lactogeneus* (contra Kottelat *et al.*, 1993; work in progress) are whitish, without any dorsal saddles at all sizes and possess an ocellated dark spot at the base of the middle caudal fin rays. Thus, it is readily distinguishable from *N. tuberigum*.

*Nemacheilus tuberigum* is easily and immediately distinguishable from *N. masyae* by colour pattern; *N. masyae* exhibits a prominent dark spot on the anterior, basal part of the dorsal fin (Smith, 1933; Kottelat, 1990: Fig. 29) which *N. tuberigum* does not.

## DISCUSSION

Squamation and tuberculation among *Nemacheilus* species varies a great deal. The specialised 'acuminate' condition of certain scales, with large apical tubercles, on the caudal peduncle of *N. selangoricus* and *N. spiniferus* as described by Inger & Chin (1962) and Kottelat (1984) is perhaps one extreme of a continuum. *Nemacheilus tuberigum* possesses elongate, tear-drop shaped scales, even if not attaining a acuminate condition, with comparatively large apical tubercles, in the same general area as *N. selangoricus* and *N. spiniferus* and other species such as *N. chrysolaimos* and *N. papillosa* also have enlarged or elongated scales on the caudal peduncle, even if these species do not possess the distinctive rows of large tubercles along the lateral line of the caudal peduncle as do the three species

just discussed. Of *N. tuberigum*, *N. chrysolaimos* and *N. papillosa* the first two have scales on the caudal peduncle that are much more elongate than those of *N. papillosa* and those of *N. tuberigum* are significantly longer than those of *N. chrysolaimos* (*N. tuberigum*  $\bar{x} = 1.59$ ,  $sd = 0.08$ ; *N. chrysolaimos*  $\bar{x} = 1.48$ ,  $sd = 0.06$  :  $t = 3.23$ ,  $p = 0.0023$ ). It is conceivable that when more species are examined in detail the gaps between different conditions of squamation found among species of *Nemacheilus* will narrow, or even disappear so that the transition between conditions will be seen as smooth.

## COMPARATIVE MATERIAL

*Nemacheilus chrysolaimos*: MZB 1374 b, 10 ex. (43.0–47.3 mm SL); Cisarua, Bogor, Java, Indonesia; Yachya, 5 April 1970. MZB 1366, 9 ex. (27.9–41.6 mm SL); Ciapus, Gadog, Bogor, Java, Indonesia; Minin, 25 December 1969. MZB 1376 b, 3 ex. (45.5–49.4 mm SL); Cimatuuk, Parung Panjang, Bogor, Java, Indonesia; S. Wargasasmita, 28 October 1970.

*Nemacheilus fasciatus*: MZB 1372 b, 3 ex., (55.3–57.6 mm SL); Cikaniki, Cipaku, Bogor, Java, Indonesia; S. Wargasasmita, 25 March 1970. MZB 1372 c, 6 ex., (56.7–69.2 mm SL); Cikaniki, Cipaku, Bogor, Java, Indonesia; S. Wargasasmita, 25 March 1970. MZB 2010, 7 ex. (56.3–68.6 mm SL), Sangharus, Airnaningan, Pulau Panggung, Lampung Selatan, Sumatra, Indonesia; D. Hardjono & F. Sabar, 26 February 1975.

*Nemacheilus jaklesii*: BMNH 1866.5.2.60, paratype, (49.1 mm SL); Paya Kumbuh, Sumatra, Indonesia; male.

*Nemacheilus papillosa*: ZMA 112.874, 2 syntypes, (48.0 mm SL, male with subocular flap obvious; 56.3 mm SL, female with eggs apparent); Lake Toba, Balige, Sumatra, Indonesia.

*Nemacheilus selangoricus*: MZB 3551, 3 ex. (28.3–29.4 mm SL); small forested stream where it flows into S. Mandai upstream from its confluence with Kapuas mainstream, S. Kapuas basin, Kalimantan Barat, Indonesia; T. Roberts, 10 August 1976. MZB 2395 b, 3 ex., (29.3–41.4 mm SL); Tanah merah, Lempake, Kalimantan, Indonesia; M. Siluba, 27 February 1978.

*Nemacheilus spiniferus*: MZB 6807, 6 ex., (32.2–37.5 mm SL); S. Tarusan, a tributary of S. Laung, a tributary of S. Barito, Kalimantan Tengah, Indonesia; D.J. Siebert, A.H. Tjakrawidjaja & O. Crimmen, 16 July 1992. MZB 6877, 11 ex., (29.5–38.0 mm SL); S. Karingian, a tributary of S. Laung, a tributary of S. Barito, Kalimantan Tengah; D.J. Siebert, A.H. Tjakrawidjaja & O. Crimmen, 7 July 1992. MZB 6928, 2 ex., (38.7–40.0 mm SL); S. Laung, a tributary of S. Barito, Laung Tuhup, Barito Utara, Kalimantan Tengah, Indonesia; D.J. Siebert, A.H. Tjakrawidjaja & O. Crimmen, 15–18 July 1992. MZB 6948, 2 ex., (34.1–34.5 mm SL); S. Mata, a tributary of S. Barito below Muara Laung, Laung Tuhup, Barito Utara, Kalimantan Tengah, Indonesia; D.J. Siebert, A.H. Tjakrawidjaja & O. Crimmen, 8 July 1992.

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*longipinnis* for us and provided translations of Ahl's description of their colour patterns. Dr. Maurice Kottelat provided valuable suggestions as a third party reviewer. Permission from Taman Nasional Gunung Leuser and Leuser Management Unit to conduct studies in the Suag Balimbing Research Station is gratefully acknowledged. We also thank the Photography Unit of the Natural History Museum, London for photographs and Abdul Mun'im for dedicated assistance with fieldwork.

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**Table 1** Morphometric and meristic data for *Nemacheilus tuberigum* sp.nov.,  $n = 28$  for paratypes; measurements follow Kottelat (1984).

	Holotype	Paratypes	$\bar{x}$	s.d.
Standard length	48.5	31.9–53.4		
Total length	122.1	121.1–127.7		
As % standard length				
Lateral length of head	22.1	20.3–24.8	22.7	0.96
Dorsal length of head	18.6	16.8–20.9	19.2	0.91
Predorsal length	48.7	47.0–52.0	49	1.36
Prepelvic length	51.2	47.9–52.8	50.4	1.20
Preanal length	75.4	73.0–78.5	75.7	1.47
Preanus length	69.2	65.1–73.3	69.4	2.11
Head height (at eye)	9.6	9.2–11.2	10.15	0.42
Body height (at nape)	12.2	11.9–14.5	12.8	0.58
Body height (at dorsal origin)	17.9	15.1–22.3	18.0	1.73
Height of caudal peduncle	10.8	10.6–11.9	11.3	0.33
Length of caudal peduncle	14.1	13.1–16.4	14.8	0.74
Snout length	8.8	7.8–9.8	8.7	0.51
Head width (at nares)	4.8	4.5–5.5	5.0	0.22
Maximum head width	12.9	12.0–14.5	7.1	0.67
Body width (at dorsal origin)	12.1	10.0–16.3	15.9	1.55
Body width (at anal origin)	6.8	6.8–8.4	24.4	0.38
Eye diameter	5.0	2.3–6.3	5.0	0.66
Interorbital width	6.3	6.3–7.9	7.1	0.37
Height of dorsal fin	15.2	12.3–20.1	15.9	2.03
Length of upper caudal lobe	21.9	21.0–28.5	24.4	1.55
Length of lower caudal lobe	24.1	22.0–26.6	23.6	1.27
Length of median caudal ray	16.8	16.0–19.8	17.5	1.09
Length of anal fin	17.4	15.4–18.2	16.8	0.75
Length of pelvic fin	15.0	14.8–17.0	15.9	0.65
Length of pectoral fin	16.6	15.7–20.8	17.8	1.25
As % dorsal head length				
Lateral length of head	118.7	111–128	118	4.52
Head height at eye	51.9	47.5–58.1	52.9	2.30
Head width at nares	26.0	23.3–28.1	26.1	1.61
Maximum head width	69.3	60.8–76.5	68.1	4.88
Eye diameter	27.2	23.9–29.9	26.5	1.48
Interorbital width	34.1	32.2–43.1	36.9	2.31
C. peduncle : Length/height	1.3	1.1–1.4	1.3	0.11
D. fin rays(simple/branched)	4/9	4/9		
Caudal fin rays	9+8	9+8		
A. fin rays (simple/branched)	3/5	3/5		
Ventral fin rays	8	8		
Pectoral fin rays	11	11		
Lateral line pores	82	76–90		

**Table 2** Comparison of selected features helpful in distinguishing *Nemacheilus tuberigum* from *N. selangoricus* and *N. spiniferus*.

	<i>N. tuberigum</i>	<i>N. selangoricus</i> *	<i>N. spiniferus</i> *
Colour Pattern	Body with 8–13 dark brown blotches, sometimes fused to form a longitudinal stripe in larger specimens. 10–15 dark brown saddles on the back, sometimes some of which are in contact with blotches on sides.	Body with 8–12 dark brown bars.	Body with 10–13 dark brown bars.
Eye diameter	Smaller, 5% SL (4.5–5.5%) 26.5% HL (23.9–29.9%)	Larger, 5.7% SL (4.7–6.9%) 29% HL (23–33%)	Larger, 6.5% SL (5.7–7.4%) 31% HL (26–33%)
Dorsal fin	Dorsal fin dusky, without spot at anterior base Height of dorsal fin shorter 15.9% SL (12.3–28.5%) 85.8% HL (65.8–108.7%)	Dorsal fin with 2 distinct black stripes and a black spot at anterior base Taller, 20.2% SL (16.4–24.9%) 101% HL (81–123%)	Dorsal fin with irregular stripes and a black spot at anterior base Taller, 20.7% SL (16.9–23.2%) 98% HL (80–113%)
Caudal fin	Upper caudal lobe, shorter 24.4% SL (21.0–18.5%) 126.5% HL (111–146.4%) Lower caudal lobe shorter 23.4% SL (15.7–20.8%) 123.4% HL (112.8–136.0%)	Longer, 33.4% SL (29.6–40.8%) 165.0% HL (144–211%) Longer, 28.8% SL (24.3–33.0%) 145.0% HL (127–158%)	Longer, 30.6% SL (26.8–34.1%) 142% HL (120–160%) Longer, 28.8% SL (23.8–34.3%) 135% HL (112–153%)
Pectoral fin	Shorter, 17.8% SL (15.7–20.8%) 92.9% HL (83.3–106.2%)	Longer, 21.1% SL (17.0–24.7%) 106% HL (92–122%)	Longer, 22.3% SL (19.1–26.7%) 105% HL (94–123%)
Lateral line pores	Complete, 82.6 (76–90)	Complete, 84.3 (77–96)	Complete, 88 (83–93)

\*Data from Kottelat (1984).



XX (340661.1)

# Revision of the western Indian Ocean fish subfamily Anisochrominae (Perciformes, Pseudochromidae)

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## CONTENTS

Introduction .....	191
Materials and Methods .....	192
Systematics .....	193
Anisochrominae Smith .....	193
<i>Anisochromis</i> Smith .....	193
<i>Anisochromis kenyae</i> Smith .....	195
<i>Anisochromis mascarenensis</i> sp.nov. ....	197
<i>Anisochromis straussi</i> Springer, Smith & Fraser .....	200
Key to species <i>Anisochromis</i> .....	202
Acknowledgements .....	202
References .....	203

**SYNOPSIS.** Monophyly of the Anisochrominae is supported by eight autapomorphies: ectopterygoid and mesopterygoid well separated from palatine; preopercle well separated from skull; dorsal insertion of posterior mandibulohyoïd ligament; dentary not forked; medial origin of A<sub>1</sub> section of adductor mandibulae; high number of epineural bones; low number of circumpeduncular scales; and low number of lower-limb gill rakers. The subfamily includes a single genus, *Anisochromis*, with three species, which are distinguished on the basis of various meristic and male coloration characters: *A. kenyae* Smith from east Africa, the Comoros Islands and Madagascar; *A. mascarenensis* sp.nov. from Réunion and Mauritius; and *A. straussi* Springer, Smith and Fraser from Saint Brandon's Shoals.

## INTRODUCTION

The family Anisochromidae was erected by Smith (1954) to accommodate a new genus and species, *Anisochromis kenyae*, from the east coast of Africa. He noted that the species exhibited pronounced sexual dichromatism, and proposed a close relationship of the new family to the Pseudochromidae. He distinguished the two families on the basis of differences in number of vertebrae, head scalation, number of lateral lines, gill membrane development, palatine dentition, fin spine development, fin-ray branching, number of pectoral-fin rays, and pelvic-fin position.

Springer *et al.* (1977) described a second species of *Anisochromis*, *A. straussi*, from Saint Brandon's Shoals (= Cargados Carajos) in the southwestern Indian Ocean, which they differentiated from *A. kenyae* on the basis of coloration and numbers of dorsal-fin rays, anal-fin rays, vertebrae and tubed lateral-line scales. They noted that the species is dimorphic, but that eggs were present in both colour forms. They therefore examined gonads of the species histologically, and concluded it is a protogynous hermaphrodite. They also investigated the systematic relationships of the Anisochromidae, and proposed that the family is the sister group of the Pseudoplesiopidae,

and that the two families form a monophyletic group with the Pseudochromidae. They therefore synonymised the three families under the oldest available name, Pseudochromidae. They noted that *Anisochromis* possessed the following autapomorphies: dorsal- and anal-fin spines very weak (versus weak to strong); no scales on head (versus head scaled); palatine teeth absent (versus present); fewer than four gill rakers on lower limb of first gill arch (versus more than seven); branchiostegal membranes with ventroposterior margins fused across ventral surface of head (versus separate ventroposteriorly); ectopterygoid and mesopterygoid well separated from palatine (versus articulate closely with palatine); and ligament from (anterior) ceratohyal attaches to dentary on coronoid process (versus at symphysis).

Godkin & Winterbottom (1985) provided evidence for classification of the Congrogadidae, previously placed in the Blennioidei or Trachinoidei, in the Pseudochromidae as the sister group of *Anisochromis*. They relegated the Congrogadidae to subfamilial status, along with the Anisochrominae, Pseudochrominae and Pseudoplesiopinae. They identified a new autapomorphy for *Anisochromis* (A<sub>1</sub> section of the adductor mandibulae originates from the preopercle medial to the dorsolateral fibres of the A<sub>2</sub> section), but noted that several of those reported by Springer *et al.*

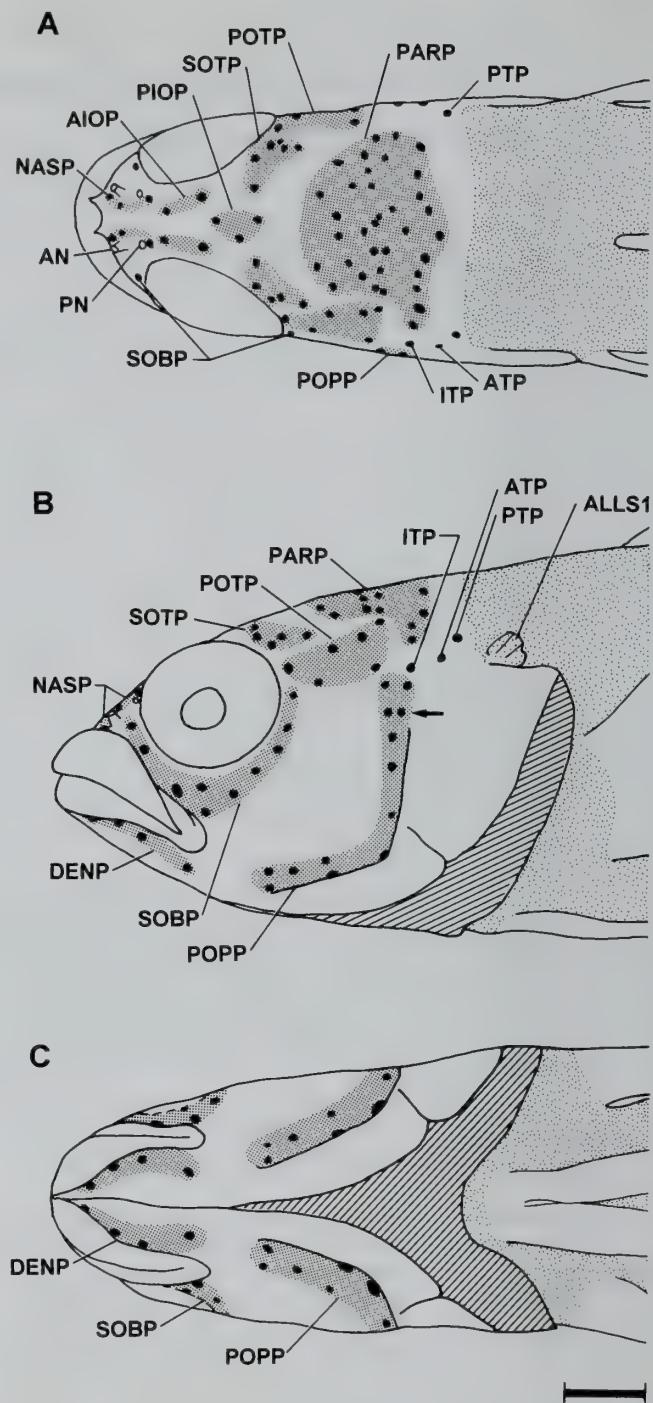
(1977) were also found in the Congrogadinae, and were thus synapomorphies of the two subfamilies: absence of palatine teeth; lower gill rakers fewer than seven; head scaleless or with scales confined to the cheek and/or operculum; and gill membranes fused.

In 1995, the first author and associates made collections of shorefishes from Mauritius. Included among the collections was a single specimen of an undescribed *Anisochromis*, which had a coloration pattern similar to *A. kenyae*, but with meristic characters more closely resembling *A. straussi*. A search of museum collections revealed a small juvenile specimen of the same species collected by J.E. Randall from the adjacent island of Réunion. In 1998, the second author made collections of shorefishes from the latter island, including nine specimens of the new species. However, he misidentified them as *A. kenyae* and recorded them as such in a checklist of the fishes of the Mascarene Islands (Fricke, 1999).

## MATERIALS AND METHODS

Institutional codes follow Leviton *et al.* (1985). All measurements to the snout tip were made to the midanterior tip of the upper lip. Length of specimens are given in mm standard length (SL), which was measured from the snout tip to the middle of the caudal peduncle at the vertical through the posterior edge of the dorsal hypural plate. Head length was measured from the snout tip to the posteriormost edge of the opercular membrane. Snout length was measured over the shortest distance from the snout tip to the orbital rim, without constricting the fleshy rim of the latter. Orbit diameter was measured as its fleshy horizontal length. Interorbital width was measured as the least fleshy width. Upper jaw length was measured from the snout tip to the posterior edge of the maxilla. Predorsal, preanal and prepelvic lengths were measured from the snout tip to the base of the first spine of the relevant fin. Body width was measured between the posttemporal pores (Fig. 1). Caudal peduncle length was measured from the base of the last anal-fin ray to the ventral edge of the caudal fin at the vertical through the posterior edge of the ventral hypural plate. Caudal peduncle depth was measured obliquely between the bases of the last dorsal- and last anal-fin rays. Measurements of fin rays excluded any filamentous membranes. Pectoral fin length was measured as the length of the longest middle ray. Caudal fin length was measured as the length of the lowermost ray on the dorsal hypural plate.

The last ray in the dorsal and anal fins is divided at its base and was counted as a single ray. As in most actinopterygians, the uppermost ray in the pectoral fins is rudimentary and rotated so that the asymmetrical medial and lateral hemitrachia appear to represent two separate rays; these were counted as a single ray. Procurrent caudal-fin ray counts were of the rays above ('upper') and below ('lower') the principal caudal-fin rays. The uppermost principal caudal-fin ray was defined as the ray articulating with hypural 5, and the lowermost principal caudal-fin ray was the ray articulating with the cartilage nubbin between the distal tips of the parhypural and the haemal spine of preural centrum 2 (= post-haemal spine cartilage of PU2 following the terminology of Fujita, 1989). Counts of tubed scales in the anterior lateral lines included both intermittent non-tubed scales and empty scale pockets; if the scale following the last tubed scale in the anterior lateral line was missing, a value for the anterior lateral line count was not recorded. 'Scales in lateral series' was defined as the number of scales in the anterior lateral line plus the number of scales rows on the caudal peduncle, the latter count beginning with the transverse row following the last tubed scale in the anterior lateral line and finishing with the transverse row passing



**Fig. 1** Cephalic laterosensory pores of *Anisochromis mascarenensis*, SMNS 23037, 23.9 mm SL, male, holotype, Réunion, in A) dorsal, B) left lateral and C) ventral views. AIOP, anterior interorbital pores; ALLS1, first anterior lateral-line scale (shown only in B; other scales omitted); AN, anterior nostril; ATP, anterior temporal pore; DENP, dentary pores; ITP, intertemporal pores; NASP, nasal pores; PARP, parietal pores; PIOP, posterior interorbital pores; PN, posterior nostril; POPP, preopercular pores; POTP, posterior otic pores; PTP, posttemporal pore; SOBP, suborbital pores; SOTP, suprotic pores. Arrow indicates dorsal tip of preopercle; branchiostegal membranes shown hatched; scaled areas on body shown in manual stipple. Scale bar = 1 mm.

through the scale at the midposterior edge of the hypural plate. 'Scales in transverse series' were counted anterodorsally from the anal-fin origin to the dorsal-fin base and are presented in the form ' $x + 1 + y = z$ ' where 'x' is the number of scales between the anterior lateral line and the anal-fin origin, '1' is the anterior lateral-line scale, 'y' is the number of scales above the anterior lateral line to the dorsal-fin base, and 'z' is the total number of scales in the series. Scale-row number for the position of the first ctenoid scale was determined by aligning the scale along an anterodorsal scale row to the anterior lateral line, then recording the number (counting from the origin of the lateral line) of the tubed scale in that row. Gill-raker counts were of the outer rakers on the first arch; the angle raker is included in the lower-limb (second) count. Counts of pseudobranch filaments included all rudiments. Because counts of gill rakers and pseudobranch filaments could not be made without damaging the branchiostegal membranes, these were only made on a few specimens.

Nomenclature of cephalic laterosensory pores is clarified in Fig. 1, and follows Winterbottom (1986), except for the nomenclature of those of the posttemporal area, which follows Gill *et al.* (2000).

Vertebral counts are given in the form precaudal + caudal = total. Caudal vertebrae are defined as those with a haemal spine, and include the terminal urostylar complex (which was counted as a single vertebra). The pattern of insertion of supraneural (predorsal) bones and anterior dorsal-fin pterygiophores within interneuronal spaces is given as an 'anterior dorsal-fin pterygiophore formula' modified from the 'predorsal formula' of Ahlstrom *et al.* (1976). Each supraneural is represented by an 'S,' neural spines are represented by slashes, and pterygiophores are represented by '2' (indicating a pterygiophore that bears a supernumerary ray and a serially associated ray), or '1' (indicating a pterygiophore that bears only a serially associated ray). A superscript 'v' indicates where a supraneural bone was present only as a vestige. Parentheses enclose elements that may be absent. An 'anterior anal-fin pterygiophore formula' is also presented, where the slashes represent haemal spines. Epineural counts are of the intermuscular bones that have been traditionally identified as epipleural ribs by perciform workers; this terminology follows Johnson & Patterson (1993: 557, 'the bones conventionally called epipleurals in those fishes [atherinomorphs and perciforms and their relatives] are homologous with the epineurals, not the epipleurals, of non-acanthomorph fishes'). Posterior epineurals were often poorly ossified, and difficult to count accurately on radiographs; counts should therefore be considered approximate. Osteological features were determined from radiographs and from cleared-and-stained specimens, which were prepared following the methods of Taylor & Van Dyke (1985). Examination of ligaments was enhanced by transfer of cleared-and-stained specimens from glycerol to 70% ethanol.

We use the terms 'female' and 'male' in preference to 'ocellated phase' and 'terminal phase' of Springer *et al.* (1977). We appreciate, however, the deficiencies of this terminology. As noted by Springer *et al.* (p. 7) for *A. straussi*: 'specimens with ocellated stage colour pattern are smaller and generally females, and specimens with terminal stage colour pattern are larger and are males, but there is considerable overlap. The overlap is not surprising and is comparable to that found in other transforming hermaphrodites.'

Count and morphometric value ranges are given first for all specimens, followed, where variation was noted, by values for the holotype in parentheses; where bilateral counts were recorded from the holotype, both counts are given and separated from each other by a slash, the first count being the left count. Frequency distributions for selected meristic characters are summarised in Tables 1–11.

## SYSTEMATICS

### ANISOCHROMINAE SMITH, 1954

Anisochromidae Smith, 1954: 298.

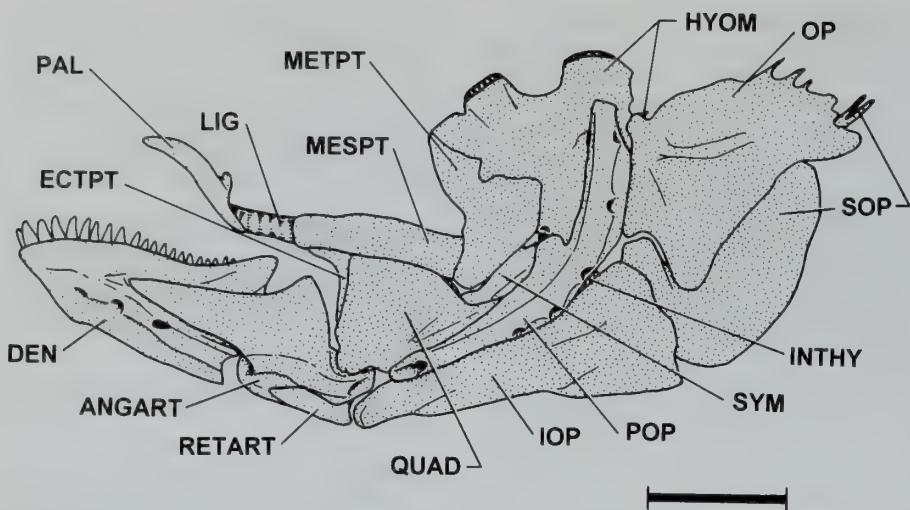
#### *Anisochromis* Smith, 1954

*Anisochromis* Smith 1954: 298 (type species, *Anisochromis kenyae* Smith, 1954, by original designation and monotypy).

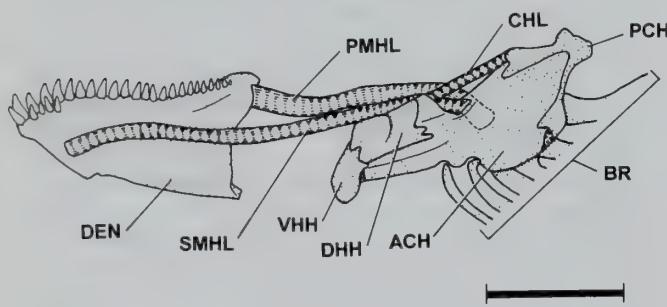
##### MONOPHYLY

The following eight autapomorphies diagnose *Anisochromis* as monophyletic:

1. *Ectopterygoid and mesopterygoid well separated from palatine.* In pseudochromines and pseudoplesiopines the palatine is loosely connected to the ectopterygoid via a short ligament and to the mesopterygoid via a short, narrow ribbon of cartilage. In congrogadines the palatine is closely applied, and often tightly bound, to the mesopterygoid; the ectopterygoid lacks an anterior process, and is disassociated from the dorsal part of the palatoquadrate (e.g., Godkin & Winterbottom, 1985: fig. 6; Gill *et al.*, 2000: fig. 3). In anisochromines the palatine is broadly separated from the ectopterygoid and mesopterygoid: the ectopterygoid is truncated anteriorly (though closely applied to the mesopterygoid), and lacks a ligamentous connection to the palatine; the mesopterygoid is connected to the palatine via a relatively long, broad, strap-like ligament (which lacks cartilage) (Fig. 2).
2. *Preopercle well separated from skull.* In congrogadines, pseudochromines and pseudoplesiopines the dorsal tip of preopercle is in close proximity to the skull, and the preopercular laterosensory canal communicates with the pterotic canal via a short membranous canal; the dorsal tip of the preopercle reaches to near the dorsal margin of the hyomandibula (e.g., Gill *et al.*, 2000: figs 1, 3). In anisochromines the preopercle is truncated dorsally, not reaching the dorsal margin of the hyomandibula (reaching to or slightly above the opercular process of the hyomandibula), and well-separated from the skull (Fig. 2); the preopercular laterosensory canal communicates with the pterotic canal via a relatively long membranous canal.
3. *Dorsal insertion of posterior mandibulohyoïd ligament.* Springer *et al.* (1977) proposed that *Anisochromis* is autapomorphic in having a modified orientation of a cord-like ligament extending from the anterior ceratohyal to the dentary, from insertion near the symphysis (pseudochromines and pseudoplesiopines) to insertion on the coronoid process. However, we present a different interpretation of this character. There are actually two more-or-less cord-like ligaments connecting the dentary and anterior ceratohyal in anisochromines, pseudochromines and pseudoplesiopines. [We use the general term 'mandibulohyoïd' for these ligaments following Greenwood (1995), though we do not intend to imply homology with the mandibulohyoïd ligaments of lower teleosts.] The first of these extends from the medial or dorsal surface of the anterior ceratohyal, in the vicinity of a dorsal notch in the bone (possibly homologous with the beryciform foramen of McAllister, 1968), to the dentary symphysis. The second mandibulohyoïd ligament extends from the lateral surface of the anterior ceratohyal at a point just anterior to the anterior/posterior ceratohyal suture to either the posterior end of the ventral process (pseudochromines and pseudoplesiopines)



**Fig. 2** Lateral view of lower jaw and suspensorium of *Anisochromis kenyae*, RUSI 4906, 23.3 mm SL, right side reversed. ANGART – angular; DEN – dentary; ECTPT – ectopterygoid; HYOM – hyomandibula; INTHY, interhyal; IOP, interopercle; LIG – ligament between palatine and mesopterygoid; MESPT, mesopterygoid; METPT, metapterygoid; OP, opercle; PAL, palatine; POP, preopercle; QUAD, quadrate; RETART, retroarticular; SOP, subopercle; SYM, symplectic. Cartilage shown in coarse stipple. Scale bar = 1 mm.



**Fig. 3** Medial view of right side dentary and hyoid bar with associated ligaments of *Anisochromis kenyae*, RUSI 4906, 23.3 mm SL. ACH, anterior ceratohyal; BR, brachiostegal rays; CHL, ligament extending between posterior and anterior ceratohyals; DEN, dentary; DHH, dorsal hypophyseal; PCH, posterior ceratohyal; PMHL, posterior mandibulohyoïd ligament (portion obscured by anterior ceratohyal shown in broken lines); SMHL, symphyseal mandibulohyoïd ligament; VHH, ventral hypophyseal. Cartilage shown in coarse stipple. Scale bar = 1 mm.

or the coronoid process (anisochromines) of the dentary (Fig. 3). We interpret this change in orientation as an autapomorphy of the Anisochrominae. Although the former (sympyseal) ligament is well-developed in congrogadines examined by us (including species of *Blennodesmus* Günther, *Congrogadus* Günther, *Halidesmus* Günther and *Haliophis* Rüppell) and in the basalmost genus *Rusichthys* Winterbottom (R.D. Mooi, pers. comm.), the latter (posterior) ligament is apparently absent (which may thus represent a synapomorphy of the Congrogadinae).

**4. Dentary not forked.** In congrogadines, pseudochromines and pseudoplesiopines, the dentary is distinctly forked posteriorly, with a relatively narrow lamina of bone connecting the prominent coronoid and ventral processes; this condition is typical of perciform fishes. In anisochromines, the coronoid and ventral processes are united by a broad lamina of bone, so that the posterior margin of the dentary is weakly concave to almost vertical (Figs 2, 3).

5. *Medial origin of A1 section of adductor mandibulae.* In pseudochromines, pseudoplesiopines and most congrogadines, a strap-like A<sub>1</sub> section of the adductor mandibulae originates from the vertical limb of the preopercle, overlying other cheek musculature (Godkin & Winterbottom, 1985: figs 1A, 1B, 1C, 2A and 2B). In some derived congrogadines, the A<sub>1</sub> section is fused to the A<sub>2</sub> section (Godkin & Winterbottom, 1985: fig. 2C). Anisochromines have a strap-like A<sub>1</sub> section, but it originates on the vertical limb of the preopercle medial to the dorsolateral fibres of the A<sub>2</sub> section (Godkin & Winterbottom, 1985: fig. 1D).
6. *High number of epineural bones.* Epineural bones are present on all precaudal vertebrae, and, depending on species, on caudal vertebrae 1 through 2–8 in pseudochromines and pseudoplesiopines (Gill, in press; Gill & Edwards, in press). Taken in the context of Gill's (1998) interpretation of intermuscular homology in congrogadines, Godkin & Winterbottom's (1985) descriptions indicate that, depending on species and specimen size, epineural bones may be confined to the first few precaudal vertebrae, or 'present as far back as the first few caudal vertebrae' in congrogadines. In anisochromines, epineural bones are present on all precaudal vertebrae, extending posteriorly on to the first 10–17 caudal vertebrae.
7. *Low number of circumpeduncular scales.* Depending on species, pseudochromines and pseudoplesiopines usually have 16 or more circumpeduncular scales; although two pseudochromine species (*Cypho zaps* Gill and *Pseudochromis striatus* Gill, Shao and Chen) may have as few as 14 circumpeduncular scales, the modal count for both is 16 (Gill, in press). Circumpeduncular counts are not obtainable in congrogadines, as the dorsal and anal fins are confluent with the caudal fin (fin condition not determined for the basal congrogadine *Rusichthys plesiomorphus* Winterbottom, but confluent in its congener *R. explicitus* Winterbottom; Winterbottom, 1996); nevertheless, congrogadines have numerous, small scales on the caudal peduncle. In anisochromines, the scales on the caudal peduncle are relatively large, with only 12–14, modally 12, circumpeduncular scales.
8. *Low number of lower-limb gill rakers.* Numbers of outer rakers on the lower limb of the gill arch (those on ceratobranchial 1 –

including the so-called angle raker – and hypobranchial 1) range from 9–17 in pseudochromines, 6–20 in pseudoplesiopines, and 5–15 in congrogadines. Anisochromines only have 2–3 lower-limb rakers, although 1–2 very tiny rudiments may be present ventral to these; all rakers and rudiments are restricted to the upper part of ceratobranchial 1. A low number of lower-limb rakers was initially proposed as a character of Anisochrominae (as Anisochromidae) by Smith (1954), and cladistically interpreted as an autapomorphy of the taxon by Springer *et al.* (1977). It was later rejected as an autapomorphy of Anisochrominae by Godkin & Winterbottom (1985) and interpreted instead as a synapomorphy of the Anisochrominae + Congrogadinae. This interpretation is problematic because counts for congrogadines broadly overlap those of pseudoplesiopines. In any case, lower-limb gill-raker counts for anisochromines are lower than has been observed in any congrogadines (some descriptions give counts as low as 4 for certain congrogadine species, but these exclude the angle raker), and we therefore interpret the very low number of lower-limb rakers in anisochromines as autapomorphic.

#### ADDITIONAL DIAGNOSTIC CHARACTERS

Additional characters useful in distinguishing anisochromines from other pseudochromids are the following: dorsal-fin rays I,25–27, all or all but first segmented rays branched; anal-fin rays I,17–19, all segmented rays branched; pectoral-fin rays 13–15; pelvic-fins rays I,4, medial ray small, inconspicuous and unbranched, all other segmented rays branched; caudal-fin rays 4–6 + 8 + 8 + 3–5 = 23–27; vertebrae 10 (rarely 11) + 22–25; head without scales (predorsal scales extending anteriorly to point ranging from about 2/3 distance from dorsal origin to parietal commissure, to just short of parietal commissure; Fig. 1); lateral line represented on body by anterodorsal series of 28–39 tubed scales, and posterolateral series of centrally pitted scales; parietal pores relatively numerous (total pores 13–44), in continuous or almost continuous series over top of head; lower lip complete (uninterrupted at symphysis) with deep symphyseal notch; branchiostegal (gill) membranes broadly united, but free from isthmus (Fig. 1); fin spines weak and flexible; and anterior dorsal-fin pterygiophore formula S/S/(S<sup>v</sup> or S) + 2/1 + 1.

#### REMARKS

We here consider the gender of *Anisochromis* to be feminine, in keeping with the accepted gender of *Chromis* [see Opinion 1417 (International Commission on Zoological Nomenclature, 1986) for ruling on the gender of *Chromis*]. Without explanation, Eschmeyer & Baily (1990: 29) gave the gender of *Anisochromis* as masculine; presumably their conclusion of masculine gender relates to the proposal by Bailey *et al.* (1980) to have all generic names ending in *-chromis* to be ruled as masculine.

#### ETYMOLOGY

The generic name is a combination of the Greek *anisos*, meaning ‘unequal’ or ‘different,’ and *Chromis*, a genus of pomacentrid fish. Gender is feminine (see Remarks above).

#### *Anisochromis kenyae* Smith, 1954

African Annie

Figs 2–7, 8A; Tables 1–11

*Anisochromis kenyae* Smith, 1954: 300, fig. 1, pl. 6 [Type locality: Malindi, Kenya; holotype RUSI 149].—Smith, 1977: 22, pl. 4C, D [taxonomic notes; range extension; colour illustrations].—Springer *et al.*, 1977: 5, fig. 1c [comparison].—Wheeler, 1985: 113 [compilation; text fig.].—Smith, 1986: 539, pl. 46, fig. 169.1A–B [compilation; colour illustrations].—Gill, 1998: fig. 5 [osteological details].—Gill & Edwards, 1999: fig. 8A [osteological details].

#### DIAGNOSIS

The following characters distinguish *A. kenyae* from congeners: dorsal-fin rays I,25–26, usually I,25; anal-fin rays I,17–18, usually I,17; caudal vertebrae 22/24, usually 23; scales in lateral series 37–44, usually 38–41; and anterior lateral-line scales 28–35, usually 30–34.

#### DESCRIPTION (based on 46 specimens, 13.8–25.6 mm SL)

Dorsal-fin rays I,25–26 (I,25), all or all but first segmented rays branched (all branched in holotype); anal-fin rays I,17–18 (I,17), all segmented rays branched; pectoral-fin rays 13–15 (14/14), upper 1–2 (1/1) and lower 0–1 (1/1) rays simple; pelvic-fin rays I,4, medial ray small, inconspicuous and unbranched, all other segmented rays branched; upper procurrent caudal-fin rays 4–6 (5); lower procurrent caudal-fin rays 4–5 (4); principal caudal-fin rays 8 + 8, upper 0–1 (0) and lower 0–2 (0) unbranched; total caudal-fin rays 24–27 (25); scales in lateral series 37–44 (38/38); anterior lateral-line scales 28–35 (31/32); anterior lateral line terminating beneath segmented dorsal-fin ray 17–21 (20/21); predorsal scales 4–8 (6); scales in transverse series 10–13 + 1 + 2–3 = 14–17 (10 + 1 + 2/10 + 1 + 2); circumpeduncular scales 12–13; gill rakers 1–2 + 2–3 = 3–5, sometimes with 1–2 tiny rudiments (inconspicuous ossifications bearing a few or no teeth) above and below rakers (gill raker count not determined in holotype); pseudobranch filaments 6–7 (not determined in holotype).

Cephalic latersensory pores (all bilaterally paired, unless otherwise stated): nasal pores 2–3 (2/2); anterior interorbital pores 2–3 (2/2); posterior interorbital pores (unpaired) 1–5 (2); supraotic pores 2–6 (5/3); suborbital pores 9–14 (10/10); posterior otic pores 1–7 (5/5); preopercular pores 8–17 (17/15); dentary pores 3–4 (4/4); intertemporal pores 1–2 (1/1); anterior temporal pores 0–1 (1/1); posttemporal pores 1–2 (2/1); total parietal pores 13–43 (36).

As percentage of standard length (based on 21 specimens, 18.5–24.5 mm SL): body depth at dorsal-fin origin 19.6–23.0 (22.5); greatest body depth 20.8–24.4 (23.0); head width 11.8–14.1 (14.1); head length 25.5–28.5 (28.2); snout length 4.6–5.6 (4.7); orbit diameter 7.1–8.7 (8.5); interorbital width 3.2–4.9 (4.2); upper jaw length 8.4–10.3 (10.3); caudal peduncle depth 13.0–15.5 (15.5); caudal peduncle length 8.0–10.6 (8.0); predorsal length 29.5–32.9 (32.9); preanal length 49.7–54.1 (54.0); prepelvic length 22.1–26.3 (26.3); first segmented dorsal-fin ray length 5.5–10.9 (9.4); third-from-last segmented dorsal-fin ray length 12.2–15.9 (14.1); dorsal-fin base length 60.5–66.5 (62.0); first segmented anal-fin ray length 5.6–10.0 (5.6); third-from-last segmented anal-fin ray length 12.9–14.8 (13.6); anal-fin base length 34.3–40.4 (37.1); caudal-fin length 19.6–22.6 (21.6); pectoral-fin length 17.3–21.7 (18.8); pelvic-fin length 12.9–17.4 (15.0).

Lower lip complete with deep symphyseal notch; fin spines weak and flexible; anterior dorsal-fin pterygiophore formula S/S/(S<sup>v</sup> or S) + 2/1 + 1 (S/S/2/1 + 1); 20–23 (22) consecutive dorsal-fin pterygiophores inserting in 1:1 relationship directly behind neural spine 4; anterior anal-fin pterygiophore formula 2/1 + 1 or /2 + 1 + 1 (2/1 + 1); 12–15 (14) consecutive anal-fin pterygiophores inserting in 1:1 relationship directly behind haemal spine 2; fourth segmented pelvic-fin ray longest; caudal fin rounded; ctenoid scales beginning at 1–7 (not determined for holotype) transverse scale rows behind branchial opening; dorsal and anal fins without distinct scale sheaths, though often with intermittent scales overlapping fin bases; intermittent series of centrally pitted scales originating on midside above anterior part of anal fin, extending posteriorly along caudal peduncle to middle part of caudal-fin base; additional 1–3 centrally pitted scales present above and below pitted scale(s) on middle part of caudal-fin base; cheeks, operculum and upper part of

head without scales; predorsal scales extending anteriorly to point ranging from about 2/3 distance from dorsal origin to parietal commissure, to just short of parietal commissure; vertebrae 10 + 22–24 (10 + 22); epurals 2; epineurals present on vertebrae 1 through 20–23 (21); pleural ribs present on vertebrae 3 through 10, the ultimate rib small to moderately developed.

Upper jaw with 3 or 4 (at symphysis) to 1 or 2 (on sides of jaw) irregular rows of small conical teeth, those of outer row much larger; lower jaw with 2 or 3 (at symphysis) to 1 (on sides of jaw) rows of small conical teeth, those of outer row much larger; vomer with 1 or 2 rows of small conical teeth arranged in chevron; palatines edentate; tongue edentate and moderately pointed.

#### LIVE COLORATION

Males (based on the description in Smith, 1954: 302, the colour illustration in Smith, 1977: pl. 4D, and a photograph of a specimen from the Comoros Islands, ROM 56501, 22.1 mm SL): head bright reddish orange to bright red, with black-edged white stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; white spot on posteroventral rim of orbit at about 3 o'clock position; narrow brown to dark grey bar extending from ventral part of orbital rim to posterior edge of maxilla; iris yellow, red centrally, with radiating brown bars; nape dark brownish red to dark grey, with scattered small white spots; body black, with scattered small white spots, these sometimes aligning to form vague bars on upper part of body; dorsal fin with large dark grey to black spot, extending from first segmented ray to about fourth or fifth segmented ray; black spot bordered anteriorly with yellow, basally with bright yellow to bright orange, and sometimes posteriorly with yellow to bright orange; basal one-third of dorsal fin behind large black spot bright red, with small black spot or streak at base of each of fin ray, these sometimes edged anteriorly with white; remainder of dorsal fin reddish or pinkish hyaline to bright red, with greyish hyaline to grey distal margin; basal one-third of anal fin bright red, with small black spot or streak at base of each of fin ray, these sometimes edged anteriorly with white; remainder of anal fin reddish or pinkish hyaline to bright red, with greyish hyaline to grey distal margin; caudal fin black basally, remainder of fin greyish hyaline to black; pectoral fin black with irregular white spots basally, remainder of fin greyish hyaline, with fin rays dark grey; pelvic fin bright yellow on base, remainder of fin black, sometimes with distal margin pale grey to hyaline. Females (based on the description in Smith, 1954: 302, the colour illustration in Smith, 1977: pl. 4C, and a photograph of a specimen from the Comoros Islands, ROM 56502, 22.7 mm SL): head olive-brown to brown dorsally, becoming pale green ventrally, with two pale olive bars on nape; large dark grey to black spot on subopercle, bordered irregularly with white, sometimes with additional, smaller white-edged black spot on lower part of subopercle; brown-edged diffuse pale olive stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; two white spots or clusters of white to mauve spots on posteroventral rim of orbit, at about 3 and 5 o'clock positions; head and nape with scattered white to mauve or pale olive small spots; narrow dark brown to grey bar extending from ventral part of orbital rim to posterior edge of maxilla; iris pale yellow to pale orange, with radiating brown bars; body generally orange-brown, becoming olive to dusky green posteriorly; body with olive-brown bars, alternating with pale olive bars; pale olive bars sometimes dotted with pale green to mauve spots; broad orange-yellow area sometimes present on side of body; upper and lower edges of caudal peduncle sometimes with small, punctate black spots; dorsal and anal fins dusky green to dusky orange or greenish hyaline, often with



**Fig. 4** *Anisochromis kenyae*, ROM 56711, 21.6 mm SL, male, Comoros Islands (Photograph by P. Hurst).

irregular pale olive to mauve or white small spots; barring on body sometimes extending slightly on to fin bases; base of each ray in dorsal and anal fins sometimes with small reddish brown to black spot or streak, edged anteriorly with pale olive to mauve or white; caudal fin olive to lime green basally, remainder of fin dusky olive to dusky orange or hyaline; fleshy pectoral-fin base maroon to dark brown, with scattered white to mauve spots; pectoral fin orangish hyaline to hyaline; pelvic fin olive, sometimes with base pale yellow.

#### PRESERVED COLORATION

Males (Figs 4, 8A): pattern generally similar to live coloration, head and anterior part of body becoming pale brown, paler ventrally; pale markings on head obsolete; dark spots and stripes on head remain, becoming dark grey-brown to dark brown; body behind pectoral-fin base dark grey-brown; white spots and bars on body remain, becoming brownish white to pale yellow; dorsal and anal fins brownish white, sometimes dusky hyaline distally, with dark grey-brown spots often present at base of each fin ray; large dark spot at anterior of dorsal fin remains, becoming dark grey-brown; caudal fin dark grey-brown basally, dusky hyaline to brown distally; pectoral fin grey-brown basally, dusky hyaline to hyaline on remainder of fin; pelvic fin brownish white to pale yellow basally, sometimes slightly darker on extreme base, remainder of fin dark grey-brown to brown, often with distal margin narrowly pale brown. Females (Fig. 5): pattern generally similar to live coloration, head and body becoming pale brown; pale markings on head and body obsolete; dark spots and stripes on head remain, becoming dark grey-brown to dark brown (ocellated spots sometimes absent, although possibly these represent intermediately coloured, sex-transforming specimens), sometimes with additional irregular brown veriform markings and spots on cheek and operculum; dark barring on head and body variably remains, becoming brown to pale brown; dark punctate spots on caudal peduncle remain, becoming dark brown to dark grey-brown, sometimes extending anteriorly to near middle of dorsal- and anal-fin bases; dorsal and anal fins dusky brown to



**Fig. 5** *Anisochromis kenyae*, ROM 56502, 22.7 mm SL, female, Comoros Islands (Photograph by P. Hurst).

brownish hyaline, often with irregular pale brown small spots; barring on body sometimes extending slightly on to fin bases; caudal fin brown to grey brown, remainder of fin dusky brown to brownish hyaline; fleshy pectoral-fin base brown, with indistinct scattered pale spots; pectoral fin brownish hyaline to hyaline; pelvic fin dusky brown to brownish hyaline, sometimes paler ventrally, usually pale brown to hyaline distally.

#### HABITAT AND DISTRIBUTION

*Anisochromis kenyae* is known only from the east coast of Africa (Kenya to northern Mozambique), the Comoros Islands and northern Madagascar (Fig. 6). As noted above, Fricke's (1999) record of the species from Réunion is based on specimens of *A. mascarenensis*. According to Smith (1954: 302), type specimens of *A. kenyae* were collected from coastal 'pools in reefs at about low-tide mark' and that they were 'not uncommon at some localities.' Data accompanying subsequently collected specimens indicate that the species also occurs on reef crests and in shallow subtidal reef areas to depths of at least 3 m.

#### COMPARISONS WITH OTHER SPECIES

The three species of *Anisochromis* differ from each other in the following meristic characters: segmented dorsal-fin rays (modally 25 in *A. kenyae* versus modally 26 in *A. mascarenensis* and *A. straussi*; Table 1); segmented anal-fin rays (modally 17 in *A. kenyae* versus modally 18 in *A. mascarenensis* and *A. straussi*; Table 1); caudal vertebrae (modally 23 in *A. kenyae* versus modally 24 in *A. mascarenensis* and *A. straussi*; Table 3); scales in lateral series (37–44, usually 38–41 in *A. kenyae* versus 40–45, usually 41–44 in *A. mascarenensis* and *A. straussi*; Table 5); anterior lateral-line scales (28–35, usually 30–34 in *A. kenyae* versus 32–39, usually 33–37 in *A. mascarenensis* and *A. straussi*; Table 6); posterior interorbital pores (1–5, usually 2–4 in *A. kenyae*, 3–4 in *A. mascarenensis*, and 1–2 in *A. straussi*; Table 11); and total parietal pores (usually more numerous in *A. kenyae* and *A. mascarenensis* than in *A. straussi*; Fig. 7).

The three species are also distinguished on the basis of preserved male coloration. The dorsal and anal fins of *A. kenyae* and *A. mascarenensis* males are generally pale (mostly red in life), with a large dark spot distally on the anterior part of the dorsal fin (Figs 4, 9). In contrast, the dorsal and anal fins of *A. straussi* males are generally dusky to black (in life and in preservative), with at most an indistinctly darker marking basally on the anterior part of the dorsal fin (Fig. 12). Probable intermediate-phase (sex-changing) specimens of *A. mascarenensis* have mostly dusky dorsal and anal fins (Fig. 11) and thus might be confused with males of *A. straussi*. However, they bear the characteristic large dark spot distally on the anterior part of the dorsal fin. The pelvic fins of *A. kenyae* and *A. mascarenensis* males are broadly pale on the basal part of the fin (though sometimes slightly darker or dappled with darker spots on the basalmost portion of the fin) and abruptly dark distally, sometimes with a pale distal margin (Figs 8A–B). In *A. straussi* males the pelvic fins are mostly dusky, although sometimes with a narrow pale basal area, with a pale distal margin (Fig. 8C). The bodies of *A. kenyae* and *A. mascarenensis* males have relatively conspicuous pale spots, whereas in *A. straussi* males pale spots are either absent, or inconspicuous and confined to the anterodorsal part of the body.

#### REMARKS

Fourmanoir (1957: 246) recorded an unidentified specimen of *Anisochromis* from Bimbini, Anjouan, Comoros Islands. Based on distribution, it would appear that his specimen, which could not be located for this study, is referable to *A. kenyae*. However, there is

reason to question the generic identity of the specimen. Although Fourmanoir gave a dorsal-fin ray count of I,25, which is characteristic of *A. kenyae* – as perhaps is his count of '35 rangées d'écaillles' (= scales in lateral series?) – his counts of anal-fin rays (I,14) and lateral-line scales (20) are well outside those known for any species of *Anisochromis*.

#### MATERIAL EXAMINED

KENYA: Shimoni, Kisiti Islands, J.L.B. & M.M. Smith, 1 November 1952, RUSI 854, 14: 17.5–25.0 mm SL (paratypes; x-radiographs only), USNM 216415 (out of RUSI 854), 6: 21.7–24.5 mm SL (paratypes); Malindi, Sail Rock channel, J.L.B. & M.M. Smith, 11 October 1952, RUSI 149, 1: 21.3 mm SL (holotype); Shimoni, J.L.B. and M.M. Smith, 27 August 1954, RUSI 4905, 3: 22.3–23.9 mm SL. TANZANIA: north-east corner of Lathan Island (06°54'05"S 039°55'43"E), rocky shore, Anton Bruun Cruise 9, Station HA-6, 20 November 1964, ANSP 134469, 1: 25.6 mm SL (x-radiograph only). MOZAMBIQUE: Pinda Reef, J.L.B. and M.M. Smith, 3 September 1956, RUSI 4906, 7: 21.6–25.0 mm SL (1: 23.3 mm SL, subsequently cleared and stained; 2: 24.0–25.0 mm SL, x-radiographs only). COMOROS ISLANDS: Moheli, reef crest off middle of bay at north-east tip of Ouenefou Island (12°23'25"S 043°42'330"E), occasional live corals (*Acropora*, *Pocillopora* and *Porites*), algae covered rubble, calcareous rock and occasional sand patches, 0–1 m, R. Winterbottom *et al.*, 22 November 1988 (field number RW 88-29), ROM 56502, 9: 13.8–22.7 mm SL; Anjouan, Point Chongochahari, headland north and east of village of M'Jamaoue (12°11'09"S 044°19'03"E), vertical coral-rock walled gully with sandy floor, small caves and crevices, and some live hard corals (*Acropora* and *Pocillopora*), 3–9 m, R. Winterbottom *et al.*, 21 November 1988 (field number RW 88-28), ROM 56711, 1: 21.6 mm SL; Mayotte, north coast of Isle Malandzamiayatsimi near eastern tip (12°40'19"S 044°03'27"E), reef top, profuse soft and hard corals (*Acropora*, *Pocillopora*, *Porites* and lettuce coral), with some calcareous rock and sand gullies, 0–4 m, W. Holleman *et al.*, 16 November 1988 (field number RW 88-17), ROM 56501, 2: 22.1–23.0 mm SL. MADAGASCAR: Nosy Bé, Andilana Beach, 100 m west of hotel, 50 m offshore (14°43'S 050°57'E), around coral bommies on sand flat with turtle grass, 0.3–2.5 m, J. Paxton, B. Collette, D. Cohen, E. Anderson, J. Nielsen and K. Sulak, 9 November 1988, AMS I.28113-064, 2: 13.9–22.1 mm SL.

#### *Anisochromis mascarenensis* sp.nov.

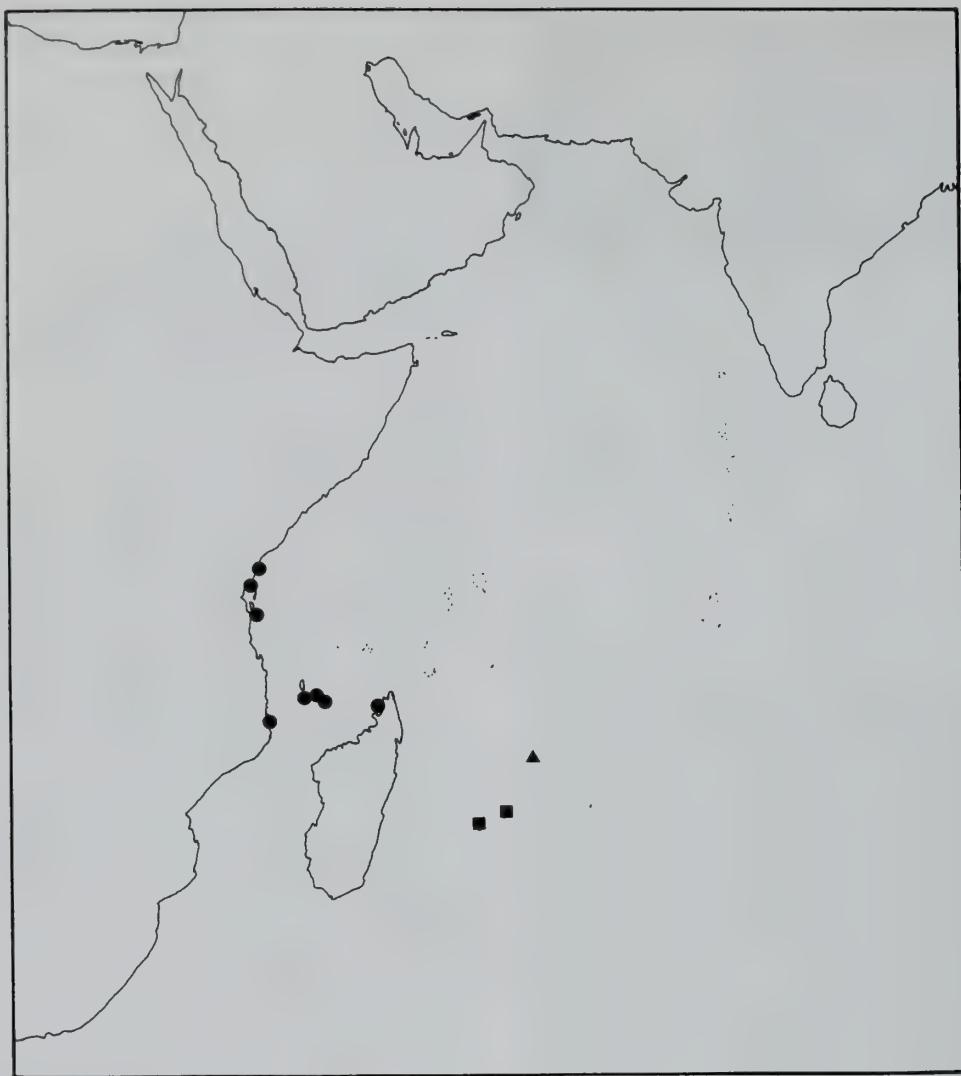
Mascarene Annie

Figs 1, 6, 7, 8B, 9–11; Tables 1–11

*Anisochromis kenyae* [non Smith, 1954].—Fricke, 1999: 214  
[Réunion].

Holotype, SMNS 23037, 23.9 mm SL, Réunion, west coast, Les Filaos, L'Hermitage-les-Bains, 11 km south-west of St-Paul, 21°06'16"S 055°12'38"E, lagoon reef with live corals, 0–0.5 m (low tide), R. Fricke, 19 December 1998.

Paratypes, BMNH 2001.3.8.2, 23.3 mm SL (subsequently cleared and stained), collected with holotype; BPBM 16277, 1: 13.3 mm SL, Réunion, Cap Houssaye, sand and coral knoll, 12–18 m, J.E. Randall, 27 October 1973; MNHN 2001-494, 24.1 mm SL, collected with holotype; SMNS 20933, 2: 19.7–25.5 mm SL, Réunion, west coast, Les Filaos, L'Hermitage-les-Bains, 11 km south-west of St-Paul, 21°06'16"S 055°12'38"E, lagoon reef with dead and live corals, 0–0.5 m (at extremely low tide), R. Fricke, 18 December 1998; SMNS 21025, 4: 19.7–25.2 mm SL, collected with holotype; USNM 364534, 19.6 mm SL, Mauritius, north coast, Grande Gaube, lagoon reef



**Fig. 6** Distributional records for *Anisochromis kenyae* (●), *A. mascarenensis* (■) and *A. straussi* (▲).

with dead and live corals, 3–4 m, P.C. Heemstra, A.C. Gill, M. Smale, W. Holleman, P. Clark and B. Galil, 16 May 1995 (field number PCH 95-M28).

#### DIAGNOSIS

The following characters distinguish *A. mascarenensis* from congeners: dorsal-fin rays I,25–26, usually I,26; anal-fin rays I,17–18, usually I,18; caudal vertebrae 23–24, usually 24; scales in lateral series 40–45, usually 42–44; posterior interorbital pores 34; total parietal pores 23–44, usually more than 30; dorsal fin of male specimens pale in preservative, with conspicuous, large dark spot distally on anterior part of fin.

#### DESCRIPTION (Based on 11 specimens, 13.3–25.5 mm SL)

Dorsal-fin rays I,25–26 (I,26), all segmented rays branched; anal-fin rays I,17–18 (I,18), all segmented rays branched; pectoral-fin rays 13–14 (13/14), upper 1 and lower 0–1 (0/1) rays simple; pelvic-fin rays I,4, medial ray small, inconspicuous and unbranched, all other segmented rays branched; upper procurent caudal-fin rays 5; lower procurent caudal-fin rays 4–5 (4); principal caudal-fin rays 8 + 8, upper 0–1 (0) and lower 0–1 (0) unbranched; total caudal-fin rays 25–26 (25); scales in lateral series 40–45 (43/43); anterior lateral

line scales 32–39 (35/35); anterior lateral line terminating beneath segmented dorsal-fin ray 19–23 (21/21); predorsal scales 5–6 (5); scales in transverse series  $10-12 + 1 + 2-3 = 13-16$  (11 + 1 + 2/11 + 1 + 2); circumpeduncular scales 12; gill rakers 1–2 + 2, sometimes with 1–2 tiny rudiments (inconspicuous ossifications bearing a few or no teeth) above and below rakers (gill raker count not determined in holotype); pseudobranch filaments 6–7 (not determined in holotype).

Cephalic laterosensory pores (all bilaterally paired, unless otherwise stated; Fig. 1): nasal pores 1–3 (3/3); anterior interorbital pores 2–3 (2/2); posterior interorbital pores (unpaired) 3–4 (3); supraotic pores 2–6 (5/6); suborbital pores 8–13 (10/10); posterior otic pores 4–10 (6/5); preopercular pores 12–18 (13/15); dentary pores 3–4 (4/4); intertemporal pores 1–2 (1/1); anterior temporal pores 1–2 (1/1); posttemporal pores 1–2 (1/1); total parietal pores 23–44 (35).

As percentage of standard length (based on nine specimens, 19.6–25.5 mm SL): body depth at dorsal-fin origin 18.7–20.8 (19.2); greatest body depth 18.7–20.8 (19.2); head width 11.5–13.3 (11.7); head length 25.2–27.4 (25.9); snout length 4.5–5.6 (5.0); orbit diameter 6.7–8.7 (7.1); interorbital width 3.3–4.1 (3.3); upper jaw

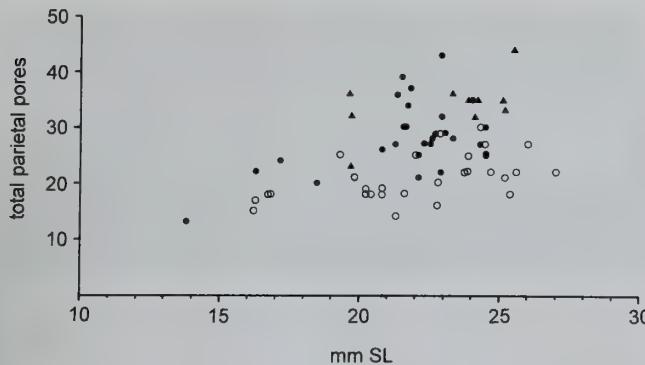


Fig. 7. Total counts of parietal pores plotted against SL for specimens of *Anisochromis kenyae* (●), *A. mascarenensis* (▲) and *A. straussi* (○).

length 8.6–9.8 (9.6); caudal peduncle depth 12.0–13.7 (13.0); caudal peduncle length 8.7–10.5 (10.5); predorsal length 28.9–31.1 (28.9); preanal length 49.6–53.9 (50.2); prepelvic length 21.2–25.5 (22.6); first segmented dorsal-fin ray length 7.8–10.0 (damaged in holotype); third-from-last segmented dorsal-fin ray length 11.6–14.5 (13.8); dorsal-fin base length 62.2–66.4 (63.6); first segmented anal-fin ray length 7.6–9.8 (8.4); third-from-last segmented anal-fin ray length 12.0–14.3 (13.8); anal-fin base length 36.9–41.2 (38.9); caudal-fin length 18.3–20.9 (20.1); pectoral-fin length 18.7–21.1 (20.1); pelvic-fin length 14.3–17.2 (17.2).

Lower lip complete with deep symphyseal notch; fin spines weak and flexible; anterior dorsal-fin pterygiophore formula  $S/S/(S^v) + 2/1 + 1$  ( $S/S/S^v + 2/1 + 1$ ); 21–23 (23) consecutive dorsal-fin pterygiophores inserting in 1:1 relationship directly behind neural spine 4; anterior anal-fin pterygiophore formula 2/1+1 or 2+1/1 (2/1+1); 13–15 (13) consecutive anal-fin pterygiophores inserting in 1:1 relationship directly behind haemal spine 2; fourth segmented pelvic-fin ray longest; caudal fin rounded; ctenoid scales beginning at 3–7 (4/3) transverse scale rows behind branchial opening; dorsal and anal fins without distinct scale sheaths, though often with intermittent scales overlapping fin bases; intermittent series of centrally pitted scales originating on midside above anterior part of anal fin, extending posteriorly along caudal peduncle to middle part of caudal-fin base; additional 1–3 centrally pitted scales present above and below pitted scale(s) on middle part of caudal-fin base; cheeks, operculum and upper part of head without scales; predorsal scales extending anteriorly to point ranging from about 2/3 distance from dorsal origin to parietal commissure, to just short of parietal commissure (Fig. 1); vertebrae 10 + 23–24 (10 + 24); epurals 2; epineurals present on vertebrae 1 through 21–24 (23); pleural ribs present on vertebrae 3 through 10, the ultimate rib small to moderately developed.

Upper jaw with 3 or 4 (at symphysis) to 1 or 2 (on sides of jaw) irregular rows of small conical teeth, those of outer row much larger; lower jaw with 2 or 3 (at symphysis) to 1 (on sides of jaw) rows of small conical teeth, those of outer row much larger; vomer with 1 or 2 rows of small conical teeth arranged in chevron; palatines edentate; tongue edentate and moderately pointed.

#### LIVE COLORATION

Males not recorded in detail, but noted to be very similar to that of *A. kenyae*. Females not recorded in detail, but noted to be very similar to that of *A. kenyae*. Probable intermediate phase specimens (based on photograph and field notes taken on paratype from Mauritius, USNM 364534, 19.6 mm SL, when freshly dead, and on field notes taken on paratype from Réunion, SMNS 20933,

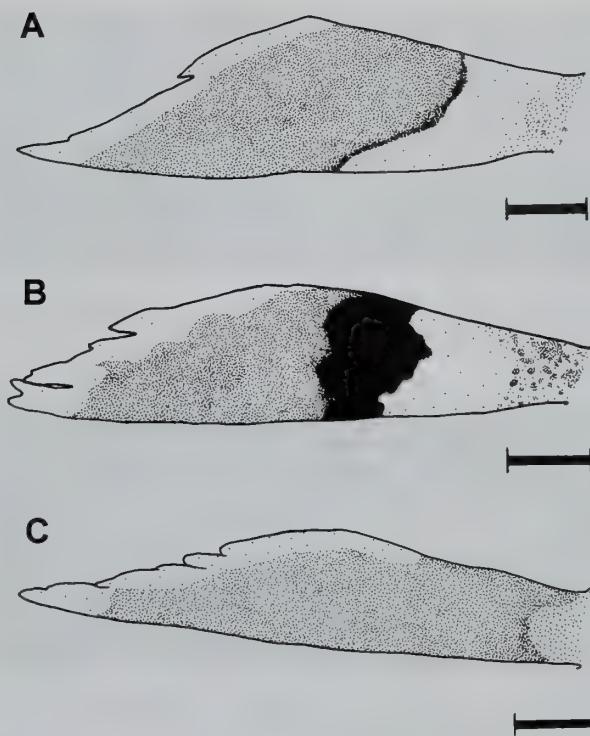
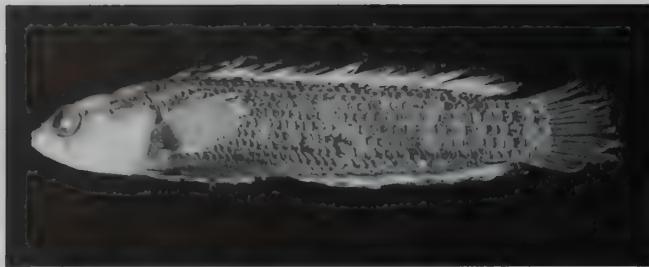


Fig. 8. Ventral view of right pelvic fin of A) *Anisochromis kenyae*, ROM 56501, 22.1 mm SL, male; B) *A. mascarenensis*, SMNS 21025, 25.2 mm SL, male paratype; C) *A. straussi*, USNM 216463, 25.2 mm SL, male paratype. Scale bars = 0.5 mm.

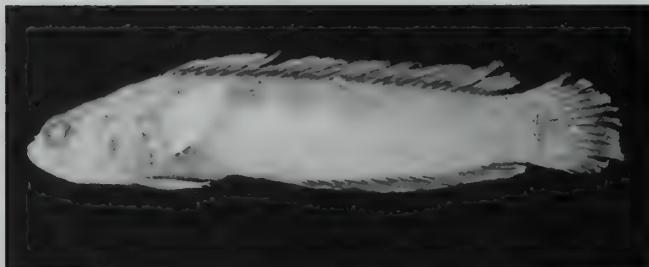
25.3 mm SL, when freshly dead): head reddish brown to bright red, with black-edged pale pink to white stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; prominent white streak at posteroventral corner of operculum, edged narrowly with black, with prominent black spot on mid-anterior edge; large white spot on middle of operculum, with scattered smaller white spots on upper edge of preopercle and on dorsoposterior part of head; white spots narrowly edged with black; two small, white spots on posteroventral rim of orbit, at about 3 and 5 o'clock positions; narrow dark grey to black bar extending from ventral part of orbital rim to posterior edge of maxilla; iris pale pink, with radiating dark brown bars; reddish brown coloration extending on to upper part of body immediately beneath lateral line, grading to dark bluish grey or black elsewhere on body; lateral-line scales pale pink; dorsal and anal fins dusky red basally, greyish hyaline distally, with white-edged black spot at base of each fin ray, anterior part of dorsal fin with large black spot, edged ventrally with orange; caudal fin dark grey basally, reddish grey on remainder of fin; fleshy pectoral-fin base and base of fin dark grey to black, with scattered white spots; remainder of pectoral fin hyaline; pelvic fin pale pinkish grey basally, grey to dark grey on remainder of fin, with pale grey to hyaline distal margin.

#### PRESERVED COLORATION

Males (Fig. 8B, 9) head pale brown, with pale stripe edged with dark grey-brown extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; narrow brown to dark grey-brown bar extending from ventral part of orbital rim to posterior edge of maxilla; nape pale brown with dark grey-brown bar across parietal commissure; body dark grey-brown to black, with scattered indistinct pale brown spots; dorsal fin with large dark

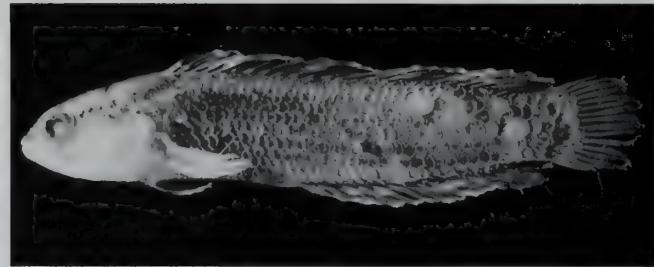


**Fig. 9.** *Anisochromis mascarenensis*, SMNS 23037, 23.9 mm SL, male, holotype, Réunion. (Photograph by P. Hurst)



**Fig. 10.** *Anisochromis mascarenensis*, SMNS 21025, 24.2 mm SL, female, paratype, Réunion. (Photograph by P. Hurst)

grey to black spot, extending from first segmented ray to about fourth or fifth segmented ray; anal fin and remainder of dorsal fin pale brown to white; basal one-quarter of dorsal and anal fins dark greyish brown, with small white spot at base of each ray; distal one-quarter of dorsal and anal fins greyish hyaline to grey; caudal fin dark grey brown to black basally, remainder of fin greyish hyaline; pectoral fin dark greyish brown to black with irregular pale brown spots basally, remainder of fin greyish hyaline, with fin rays dark grey; pelvic fin with broad pale brown band near base of fin, edged basally with narrow slightly darker band or dappled spots and distally with dark grey (which is darkest immediately adjacent to pale band), distal edge of fin pale grey-brown. Females (Fig. 10): head brown dorsally, paler ventrally, with two or three dark brown bars on nape; large dark brown to dark grey-brown spot on subopercle, bordered irregularly with pale brown, sometimes with additional, smaller pale-edged dark brown spot on lower part of subopercle; brown-edged diffuse pale brown stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; cheek and operculum sometimes with irregular brown vermiciform markings and spots; narrow dark brown to grey-brown bar extending from ventral part of orbital rim to posterior edge of maxilla; body pale brown; upper part of body with brown to grey-brown bars, becoming less distinct ventrally; broad pale yellow to pale brown area sometimes present on side of body; upper and lower edges of caudal peduncle sometimes with small, punctate black spots; dorsal and anal fins dusky brown to brownish hyaline, often with irregular pale brown small spots; barring on body sometimes extending slightly on to fin bases; caudal fin brown to grey brown, remainder of fin dusky brown to brownish hyaline; fleshy pectoral-fin base brown, with scattered pale spots; pectoral fin brownish hyaline to hyaline; pelvic fin dusky brown, pale brown distally. Probable intermediate phase specimens (Fig. 11): pattern generally similar to live coloration, reddish brown and red areas on head, body and fins become pale brown; white spots and markings on head, body and fins less distinct, becoming pale grey to pale yellowish



**Fig. 11.** *Anisochromis mascarenensis*, SMNS 20933, 25.5 mm SL, sexually transforming individual(?), paratype, Réunion. (Photograph by P. Hurst)

brown; dark spots and markings on head, body and fins become dark brown to dark grey-brown; indistinct dark spot or ocellated dark spot (as in females) variably present on subopercle; body either more-or-less uniformly dark grey-brown (except for pale spots) or dark grey-brown with narrow pale brown bands; pelvic fins mostly dusky brown to dark grey-brown, with broad pale band near fin base and pale brown to hyaline distal margin.

#### HABITAT AND DISTRIBUTION

*Anisochromis mascarenensis* is known only from Réunion and Mauritius, Mascarene Islands (Fig. 6). It has been collected from lagoon reefs with live and dead corals in 0–18 m. Most specimens collected by the second author at Réunion emerged from the base of live, branched *Acropora*.

#### COMPARISONS WITH OTHER SPECIES

See under *A. kenyae*.

#### REMARKS

*Anisochromis mascarenensis* is apparently not common in Mauritius. The first author and associates made 13 rotenone stations in apparently appropriate habitat (around shallow lagoonal reefs) in Mauritius, but collected only a single specimen.

#### ETYMOLOGY

The specific epithet alludes to the distribution of the species.

#### MATERIAL EXAMINED

See above under type material.

#### *Anisochromis straussi* Springer, Smith & Fraser, 1977

Saint Brandon's Annie

Figs 6, 7, 8C, 12–13; Tables 1–11

*Anisochromis straussi* Springer, Smith & Fraser, 1977: 2, figs 1a, 1b and 2 [type locality: 2 miles east of Raphael Island, Saint Brandon's Shoals; holotype USNM 21642].—Godkin & Winterbottom, 1985: 634, fig. 1D [osteological and myological comparison]—Mooi, 1990: 457, tables 1, 3, fig. 2e [egg surface morphology].

#### DIAGNOSIS

The following characters distinguish *A. straussi* from congeners: dorsal-fin rays I, 25–27, usually I, 26; anal-fin rays I, 17–19, usually I, 18; caudal vertebrae 23–25, usually 24; scales in lateral series 41–45, usually 41–44; anterior lateral-line scales 32–39, usually 33–37; posterior interorbital pores 1–2; total parietal pores 14–30; and dorsal fin of male specimens generally dusky in preservative, without large dark spot on anterior part of fin.

#### DESCRIPTION (Based on 82 specimens, 16.1–28.3 mm SL)

Dorsal-fin rays I, 25–27 (I, 26), all segmented rays branched; anal-fin rays I, 17–19 (I, 18), all segmented rays branched; pectoral-fin rays

13–15 (14/14), upper 1–2 (1/1) and lower 0–1 (0/0) rays simple; pelvic-fin rays I,4, medial ray small, inconspicuous and unbranched, all other segmented rays branched; upper procurrent caudal-fin rays 4–6 (5); lower procurrent caudal-fin rays 3–4 (4); principal caudal-fin rays 8 + 8, upper 0–1 (0) and lower 0–1 (0) unbranched; total caudal-fin rays 23–26 (25); scales in lateral series 41–45 (43/43); anterior lateral-line scales 32–39 (32/34); anterior lateral line terminating beneath segmented dorsal-fin ray 18–24 (18/19); predorsal scales 4–7 (6); scales in transverse series 11–14 + 1 + 2–3 = 14–18 (12 + 1 + 3/13 + 1 + 2); circumpeduncular scales 12–14 (12); gill rakers 2 + 2–3, sometimes with 1–2 tiny rudiments (inconspicuous ossifications bearing a few or no teeth) above and below rakers (gill raker count not determined in holotype); pseudobranch filaments 6–7 (not determined in holotype).

Cephalic laterosensory pores (all bilaterally paired, unless otherwise stated): nasal pores 2–3 (2/2); anterior interorbital pores 1–3 (2/2); posterior interorbital pores (unpaired) 1–2 (2); supraotic pores 1–3 (3/2); suborbital pores 8–13 (12/11); posterior otic pores 2–7 (3/2); preopercular pores 9–15 (13/13); dentary pores 3–4 (4/4); intertemporal pores 1–2 (1/1); anterior temporal pores 0–1 (1/1); posttemporal pores 1; total parietal pores 14–30 (25).

As percentage of standard length (based on 20 specimens, 16.7–27.0 mm SL): body depth at dorsal-fin origin 19.2–21.8 (21.8); greatest body depth 20.6–23.8 (23.8); head width 11.5–13.7 (12.1); head length 24.6–28.6 (27.2); snout length 4.2–5.7 (5.4); orbit diameter 6.5–9.0 (7.1); interorbital width 3.3–4.5 (3.8); upper jaw length 9.1–10.5 (10.5); caudal peduncle depth 12.7–15.6 (14.2); caudal peduncle length 8.2–10.7 (9.6); predorsal length 27.7–31.7 (30.5); preanal length 48.9–52.9 (49.8); prepelvic length 22.6–25.7 (23.4); first segmented dorsal-fin ray length 7.9–10.1 (7.9); third-from-last segmented dorsal-fin ray length 11.7–14.9 (14.2); dorsal-fin base length 62.0–66.9 (66.9); first segmented anal-fin ray length 6.9–8.9 (7.1); third-from-last segmented anal-fin ray length 12.3–14.4 (13.8); anal-fin base length 38.1–41.8 (41.0); caudal-fin length 17.8–20.7 (20.5); pectoral-fin length 15.9–20.8 (19.2); pelvic-fin length 10.5–17.8 (15.1).

Lower lip complete with deep symphyseal notch; fin spines weak and flexible; anterior dorsal-fin pterygiophore formula S/S/(S') + 2/1 + 1 (S/S/2/1 + 1); 21–24 (23) consecutive dorsal-fin pterygiophores inserting in 1:1 relationship directly behind neural spine 4; anterior anal-fin pterygiophore formula 2/1 + 1, 2 + 1/1 or 2 + 1 + 1/1 (2/1 + 1); 12–16 (13) consecutive anal-fin pterygiophores inserting in 1:1 relationship directly behind haemal spine 2; fourth segmented pelvic-fin ray longest; caudal fin rounded; ctenoid scales beginning at 3–14 (4/3) transverse scale rows behind branchial opening; dorsal and anal fins without distinct scale sheaths, though often with intermittent scales overlapping fin bases; intermittent series of centrally pitted scales originating on midside above anterior part of anal fin, extending posteriorly along caudal peduncle to middle part of caudal-fin base; additional 1–3 centrally pitted scales present above and below pitted scale(s) on middle part of caudal-fin base; cheeks, operculum and upper part of head without scales; predorsal scales extending anteriorly to point ranging from about 2/3 distance from dorsal origin to parietal commissure, to just short of parietal commissure; vertebrae 10–11 + 23–25 = 33–35 (10 + 24); epurals 2; epineurals present on vertebrae 1 through 20–27 (22); pleural ribs present on vertebrae 3 through 10, the ultimate rib very small to moderately developed.

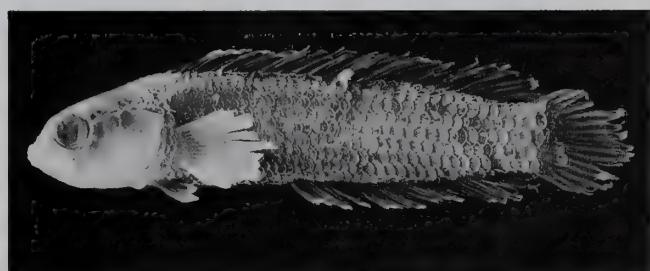
Upper jaw with 3 or 4 (at symphysis) to 1 or 2 (on sides of jaw) irregular rows of small conical teeth, those of outer row much larger; lower jaw with 2 or 3 (at symphysis) to 1 (on sides of jaw) rows of small conical teeth, those of outer row much larger; vomer with 1 or 2 rows of small conical teeth arranged in chevron; palatines edentate; tongue edentate and moderately pointed.

#### LIVE COLORATION

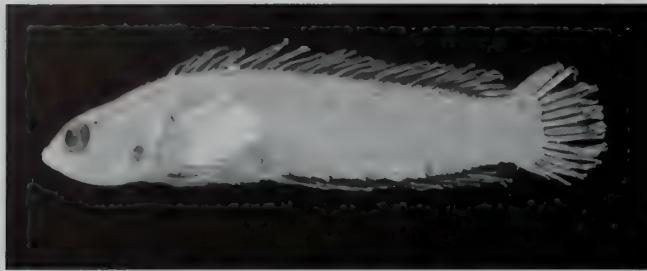
Males (based on a photograph of a probable paratype, and on the description given by Springer *et al.*, 1977: 4) head bright reddish orange, with black-edged white stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; two white spots on posteroventral rim of orbit, at about 3 and 5 o'clock positions; narrow dark grey bar extending from ventral part of orbital rim to posterior edge of maxilla; iris yellow, red centrally, with radiating brown bars; reddish orange coloration extending slightly on to anterior part of body, rapidly grading to uniform black; dorsal, anal and caudal fins black basally, becoming grey to greyish hyaline on distal margin; base of dorsal fin with small, intermittent pale grey spots; pectoral fin dark grey to black basally, remainder of fin greyish hyaline, with fin rays dark grey; pelvic fin black, with distal margin pale grey to hyaline. Females (based on photographs of two probable paratypes, and on the description given by Springer *et al.*, 1977: 4) head olive-brown to brown dorsally, becoming pale green to lime green ventrally, with two pale olive bars on nape; large dark grey to black spot on subopercle, bordered irregularly with white; black-edged white stripe extending from posterodorsal rim of orbit, above upper part of preopercle, to upper edge of operculum; two white spots or clusters of white spots on posteroventral rim of orbit, at about 3 and 5 o'clock positions; narrow dark brown to grey bar extending from ventral part of orbital rim to posterior edge of maxilla; iris red, with radiating brown bars; body generally orange-brown, becoming olive to dusky green posteriorly; dorsal part of body with short, indistinct olive-brown bars, alternating with pale olive to orange-brown bars; pale olive to orange-brown bars sometimes extending on to lower part of body, becoming pale pink ventrally; broad orange-yellow area often present on side of body; dorsal and anal fins dusky green to dusky orange; barring on upper part of body extending slightly on to dorsal-fin base; dark bars on posterior part of dorsal-fin base sometimes bearing dark grey to black punctate spots; distal margins of dorsal and anal fins abruptly pale grey to hyaline; caudal fin olive to lime green basally, remainder of fin dusky olive to dusky orange; fleshy pectoral-fin base dusky orange to dusky olive, with scattered small white spots; pectoral fin lime green basally, becoming greenish to orangish hyaline distally; pelvic fin olive to grey basally, remainder of fin dark olive to dark grey, with pale grey to hyaline distal margin.

#### PRESERVED COLORATION

Males (Fig. 8C, 12): pattern generally similar to live coloration, head and anterior part of body becoming pale brown, paler ventrally; pale markings on head obsolete; dark spots and stripes on head remain, though sometimes faint, becoming brown to dark grey-brown; body behind pectoral-fin base dark grey-brown; several indistinct pale brown spots sometimes present on anterodorsal part



**Fig. 12.** *Anisochromis straussi*, USNM 216463, 24.7 mm SL, male, paratype, Saint Brandon's Shoals. (Photograph by P. Hurst)



**Fig. 13.** *Anisochromis straussi*, USNM 216463, 22.8 mm SL, female, paratype, Saint Brandon's Shoals. (Photograph by P. Hurst)

of body; coloration of fins similar to when live; pale brown spots often present at base of each dorsal-fin ray; several pale brown spots sometimes present basally on anterior part of dorsal fin. Females (Fig. 13): pattern generally similar to live coloration, head and body becoming pale brown; pale markings on head and body indistinct or absent; dark spots and stripes on head mostly remain, becoming dark grey-brown to dark brown (ocellated spots sometimes absent, though possibly these represent intermediately coloured, sex-transforming specimens), sometimes with additional irregular brown spots and markings on cheek and operculum; dark barring on head and body variably remains, becoming brown to pale brown; dark punctate spots on caudal peduncle remain, becoming dark brown to dark grey-brown, sometimes extending anteriorly to near middle of dorsal- and anal-fin bases, occasionally extending on to sides of body; dorsal and anal fins dusky brown to brownish hyaline, often with irregular pale brown small spots; barring on body sometimes extending slightly on to fin bases; caudal fin pale brown, remainder of fin pale brown to hyaline; pectoral-fin base pale brown, remainder of fin pale brown to hyaline; pelvic fin dusky brown to brownish hyaline, paler on base and distal margin.

#### HABITAT AND DISTRIBUTION

*Anisochromis straussi* is known only from Saint Brandon's Shoals (Fig. 6). According to Springer *et al.* (1977: 6), it was collected in 0.25–11 m from rocky reefs that included dead and live coral, proximate to areas exposed at low tide. They further noted that 'specimens of *A. straussi* were lying on the bottom adjacent to isolated, small (perhaps less than 0.5 meter in diameter), live coral heads with surfaces composed of tiny finger-like projections. Our presumption is that the *Anisochromis* were living in the corals.'

#### COMPARISONS WITH OTHER SPECIES

See under *A. kenyae*.

#### REMARKS

Springer *et al.* (1977) gave a standard length of 25.5 mm for the holotype of *A. straussi*, whereas we measured it as only 23.9 mm.

#### MATERIAL EXAMINED

Saint Brandon's Shoals (= Cargados Carajos) Lagoon at Tortue Island (16°19'S 059°41'E), 0.15 m (stated depth 0.5 feet), V.G. Springer *et al.*, 7 April 1976 (field number VGS 76-11), USNM 216463, 19: 16.2–27.0 mm SL (paratypes); 2 miles east of Raphael Island (16°20'S 059°38.5'E), inside edge of reef flat, 0.15–1.05 m (stated depth 0.5–3.5 feet), V.G. Springer *et al.*, 3 April 1976 (field number VGS 76-7), USNM 216462, 1: 23.9 mm SL (holotype), USNM 215859, 26: 18.7–26.1 mm SL (paratypes; x-radiographs only); off northern tip of Saint Brandon's Shoals, ca. 16°25'S 59°36'E, rocky reef with some live coral and some channels and white coarse sand bottom, 6–10.5 m (stated depth 20–35 feet), V.G. Springer *et al.*, 6 April 1976 (field number VGS 76-10), BMNH

1976.8.24.1–10, 10: 16.8–25.4 mm SL (paratypes; 21.5 mm SL paratype subsequently cleared and stained); about 100 yards off west side of Raphael Island (ca. 16°26'S 059°36'E), coral patch in surge channel, 0–7.5 m (stated depth 0–25 feet), V.G. Springer *et al.*, 2 April 1976 (field number VGS 76-6), USNM 216464, 1: 26.8 mm SL (paratype; x-radiograph only); lagoon south of Raphael Island (ca. 16°28'S 059°37'E), live and dead coral reef surrounded by fine white sand, 0–3.6 m (stated depth 0–12 feet), V.G. Springer *et al.*, 8 April 1976 (field number VGS 76-12), USNM 216466, 2: 26.5–28.3 mm SL (paratypes; x-radiographs only); along southeast side of Grande Passe (ca. 16°28'S 059°40'E), face and channels of reef, 0–6 m (stated depth 0–20 feet), V.G. Springer *et al.*, 5 April 1976 (field number VGS 76-9), CAS 37640, 14: 16.1–24.9 mm SL (paratypes; x-radiographs only); ca. 16°32'S 059°41'E, 0–2 m, V.G. Springer *et al.*, 30 March 1976 (field number VGS 76-1), USNM 216465, 3: 22.6–23.9 mm SL (paratypes; x-radiographs only); ca. 16°43'S 059°35'E, live coral reef with dead rock and coral, rubble shore, 0–1.2 m (stated depth 0–4 feet), V.G. Springer *et al.*, 11 April 1976 (field number VGS 76-17), AMNH 35892, 6: 22.0–28.0 mm SL (paratypes; x-radiographs only).

#### KEY TO SPECIES OF ANISOCHROMIS

- 1a. Dorsal-fin rays I,25–26, usually I,25; anal-fin rays I,17–18, usually I,17; caudal vertebrae 22–24, usually 23; scales in lateral series 37–44, usually 38–41; anterior lateral-line scales 28–35, usually 30–34 (east Africa, Comoros Islands and Madagascar) ..... *kenyae* Smith
- 1b. Dorsal-fin rays I,25–27, usually I,26; anal-fin rays I,17–19, usually I,18; caudal vertebrae 23–25, usually 24; scales in lateral series 40–45, usually 41–44; anterior lateral-line scales 32–39, usually 33–37 ..... 2
- 2a. Dorsal fin of male specimens pale in preservative, with conspicuous, large dark spot distally on anterior part of fin; pelvic fins of preserved males broadly pale on basal part of fin (sometimes slightly darker or dappled with darker spots on basalmost portion of fin) and abruptly dark distally, sometimes with pale distal margin; posterior interorbital pores 3–4; total parietal pores 23–44, usually more than 30 (Réunion and Mauritius) ..... *mascarenensis* sp.nov.
- 2b. Dorsal fin of male specimens generally dusky in preservative, without large dark spot on anterior part of fin; pelvic fins of males mostly dusky in preservative, although sometimes with narrow pale basal area, with pale distal margin; posterior interorbital pores 1–2; total parietal pores 14–30 (Saint Brandon's Shoals) ..... *strausii* Springer, Smith & Fraser

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**Table 1** Frequency distributions of dorsal-, anal- and pectoral-fin-ray counts for *Anisochromis* species. Bilateral counts of pectoral-fin rays are included.

	Segmented D rays					Segmented A rays					Pectoral rays				
	25	26	27	$\bar{x}$	SD	17	18	19	$\bar{x}$	SD	13	14	15	$\bar{x}$	SD
<i>A. kenyae</i>															
Kenya	22	2	–	25.1	0.3	23	1	–	17.0	0.2	1	15	4	14.2	0.5
Tanzania	1	–	–			1	–	–			No data taken				
Mozambique	7	–	–	25.0	0.0	7	–	–	17.0	0.0	1	9	–	13.9	0.3
Comoros	9	3	–	25.3	0.5	10	2	–	17.2	0.4	4	20	–	13.8	0.4
Madagascar	–	1	–			1	1	–	17.5	0.7	–	4	–	14.0	0.0
Total	39	6	–	25.1	0.3	42	4	–	17.1	0.3	6	48	4	14.0	0.4
<i>A. mascarenensis</i>															
Réunion	1	9	–	25.9	0.3	2	8	–	17.8	0.4	7	13	–	13.7	0.5
Mauritius	–	1	–			–	1	–			2	–	–	13.0	0.0
Total	1	10	–	25.9	0.3	2	9	–	17.8	0.4	9	13	–	13.6	0.5
<i>A. straussi</i>	10	69	2	25.9	0.4	5	74	2	18.0	0.3	8	51	1	13.9	0.4

**Table 2** Frequency distributions of caudal-fin-ray counts for *Anisochromis* species.

	4	5	Upper 6	$\bar{x}$	SD	3	4	Lower 5	$\bar{x}$	SD
<i>A. kenyae</i>										
Kenya	1	20	2	5.0	0.4	—	17	6	4.3	0.4
Tanzania	—	1	—	—	—	—	1	—	—	—
Mozambique	—	5	1	5.2	0.4	—	6	1	4.1	0.4
Comoros	—	10	2	5.2	0.4	—	8	4	4.3	0.5
Madagascar	—	2	—	5.0	0.0	—	2	—	4.0	0.0
Total	1	38	5	5.1	0.4	—	34	11	4.2	0.4
<i>A. mascarenensis</i>										
Réunion	—	10	—	5.0	0.0	—	8	2	4.2	0.4
Mauritius	—	1	—	—	—	—	1	—	—	—
Total	—	11	—	5.0	0.0	—	9	2	4.2	0.4
<i>A. straussi</i>										
	3	74	2	5.0	0.3	1	78	—	4.0	0.1
	23	24	25	26	27	$\bar{x}$	SD			
<i>A. kenyae</i>										
Kenya	—	1	15	6	1	25.3	0.6	—	—	—
Tanzania	—	—	1	—	—	—	—	—	—	—
Mozambique	—	—	4	2	—	25.3	0.5	—	—	—
Comoros	—	—	8	2	2	25.5	0.8	—	—	—
Madagascar	—	—	2	—	—	25.0	0.0	—	—	—
Total	—	1	30	10	3	25.3	0.6	—	—	—
<i>A. mascarenensis</i>										
Réunion	—	—	8	2	—	25.2	0.4	—	—	—
Mauritius	—	—	1	—	—	—	—	—	—	—
Total	—	—	9	2	—	25.2	0.4	—	—	—
<i>A. straussi</i>										
	1	2	72	2	—	25.0	0.3	—	—	—

**Table 3** Frequency distributions of vertebral counts for *Anisochromis* species.

	10	11	Precaudal $\bar{x}$	SD	22	23	24	Caudal 25	$\bar{x}$	SD
<i>A. kenyae</i>										
Kenya	24	—	10.0	0.0	2	21	1	—	23.0	0.4
Tanzania	1	—	—	—	—	1	—	—	—	—
Mozambique	7	—	10.0	0.0	1	6	—	—	22.9	0.4
Comoros	12	—	10.0	0.0	1	11	—	—	22.9	0.3
Madagascar	2	—	10.0	0.0	—	1	1	—	23.5	0.7
Total	46	—	10.0	0.0	4	40	2	—	23.0	0.4
<i>A. mascarenensis</i>										
Réunion	10	—	10.0	0.0	—	2	8	—	23.8	0.4
Mauritius	1	—	—	—	—	—	1	—	—	—
Total	11	—	10.0	0.0	—	2	9	—	23.8	0.4
<i>A. straussi</i>										
	79	2	10.0	0.2	—	12	68	1	23.9	0.4
	32	33	34	35	$\bar{x}$	SD				
<i>A. kenyae</i>										
Kenya	2	21	1	—	33.0	0.4	—	—	—	—
Tanzania	—	1	—	—	—	—	—	—	—	—
Mozambique	1	6	—	—	32.9	0.4	—	—	—	—
Comoros	1	11	—	—	32.9	0.3	—	—	—	—
Madagascar	—	1	1	—	33.5	0.7	—	—	—	—
Total	4	40	2	—	33.0	0.4	—	—	—	—
<i>A. mascarenensis</i>										
Réunion	—	2	8	—	33.8	0.4	—	—	—	—
Mauritius	—	—	1	—	—	—	—	—	—	—
Total	—	2	9	—	33.8	0.4	—	—	—	—
<i>A. straussi</i>										
	—	10	70	1	33.9	0.4	—	—	—	—
	32	33	34	35	$\bar{x}$	SD				

**Table 4** Frequency distributions of numbers of consecutive dorsal-fin pterygiophores inserting in 1:1 relationship with interneural spaces directly behind neural spine 4, and anal-fin pterygiophores inserting in 1:1 relationship with interhaemal spaces directly behind haemal spine 2 for species of *Anisochromis*.

	20	21	1:1 D pterygiophores			$\bar{x}$	SD	12	13	1:1 A pterygiophores			$\bar{x}$	SD
			22	23	24					14	15	16		
<i>A. kenyae</i>														
Kenya	1	1	21	1	—	21.9	0.5	1	—	22	1	—	14.0	0.5
Tanzania	—	—	1	—	—			—	—	1	—	—		
Mozambique	—	—	7	—	—	22.0	0.0	1	—	6	—	—	13.7	0.8
Comoros	1	2	7	—	—	21.6	0.7	3	2	4	—	—	13.1	0.9
Madagascar	—	—	1	—	—			—	—	1	1	—	14.5	0.7
Total	—	2	37	1	—	21.9	0.5	5	2	34	2	—	13.8	0.7
<i>A. mascarenensis</i>														
Réunion	—	2	2	5	—	22.3	0.9	—	3	2	4	—	14.1	0.9
Mauritius	—	—	1	—	—			—	—	—	1	—		
Total	—	2	3	5	—	22.3	0.8	—	3	2	5	—	14.2	0.9
<i>A. straussi</i>														
	—	14	8	57	2	22.6	0.8	1	23	6	48	1	14.3	1.0

**Table 5** Frequency distributions of counts of scales in lateral series for *Anisochromis* species. Bilateral counts are included.

	37	38	39	40	41	42	43	44	45	$\bar{x}$	SD
<i>A. kenyae</i>											
Kenya	—	2	5	5	4	2	1	1	—	40.3	1.6
Mozambique	—	—	3	3	3	1	—	—	—	40.2	1.0
Comoros	1	4	7	8	4	—	—	—	—	39.4	1.1
Madagascar	—	—	2	1	1	—	—	—	—	39.8	1.0
Total	1	6	17	17	12	3	1	1	—	39.9	1.3
<i>A. mascarenensis</i>											
Réunion	—	—	—	1	—	5	4	5	2	43.1	1.3
Mauritius	—	—	—	—	—	1	—	1	—	43.0	1.4
Total	—	—	—	1	—	6	4	6	2	43.1	1.3
<i>A. straussi</i>											
	—	—	—	—	6	19	20	13	1	42.7	1.0

**Table 6** Frequency distributions of counts of anterior lateral-line scales for *Anisochromis* species. Bilateral counts are included.

	28	29	30	31	32	33	34	35	36	37	38	39	$\bar{x}$	SD
<i>A. kenyae</i>														
Kenya	1	1	3	4	1	—	3	1	—	—	—	—	31.4	2.1
Mozambique	—	—	1	2	1	4	1	—	—	—	—	—	32.2	1.3
Comoros	3	2	4	5	4	3	—	—	—	—	—	—	30.7	1.6
Madagascar	—	—	1	2	1	—	—	—	—	—	—	—	31.0	0.8
Total	4	3	9	13	7	7	4	1	—	—	—	—	31.2	1.7
<i>A. mascarenensis</i>														
Réunion	—	—	—	—	1	2	2	7	3	1	1	1	35.2	1.7
Mauritius	—	—	—	—	—	—	—	1	1	—	—	—	35.5	0.7
Total	—	—	—	—	1	2	2	8	4	1	1	1	35.2	1.6
<i>A. straussi</i>														
	—	—	—	—	2	7	13	12	10	6	3	1	35.0	1.6

**Table 7** Frequency distributions of anterior lateral-line termination positions (relative to segmented dorsal-fin rays) for *Anisochromis* species. Bilateral counts are included.

	17	18	19	20	Segmented dorsal-fin ray				$\bar{x}$	SD
					21	22	23	24		
<i>A. kenyae</i>										
Kenya	1	4	4	3	2	—	—	—	19.1	1.2
Mozambique	—	1	3	3	2	—	—	—	19.7	1.0
Comoros	2	3	9	3	4	—	—	—	19.2	1.2
Madagascar	—	—	—	2	—	—	—	—	20.0	0.0
Total	3	8	16	11	8	—	—	—	19.3	1.1
<i>A. mascarenensis</i>										
Réunion	—	—	1	5	6	4	2	—	21.1	1.1
Mauritius	—	—	—	—	1	1	—	—	21.5	0.7
Total	—	—	1	5	7	5	2	—	21.1	1.1
<i>A. straussi</i>										
	—	1	3	9	19	12	9	1	21.3	1.3

**Table 8** Frequency distributions of counts of scales in transverse series for *Anisochromis* species. Bilateral counts are included.

	10	11	12	13	14	$\bar{x}$	SD	2	3	$\bar{x}$	SD
<i>A. kenyae</i>											
Kenya	7	7	4	1	—	10.9	0.9	19	1	2.1	0.2
Mozambique	4	6	—	—	—	10.6	0.5	9	1	2.1	0.3
Comoros	5	13	6	—	—	11.0	0.7	24	—	2.0	0.0
Madagascar	2	1	1	—	—	10.8	1.0	4	—	2.0	0.0
Total	18	27	11	1	—	10.9	0.8	56	2	2.0	0.2
<i>A. mascarenensis</i>											
Réunion	—	11	7	—	—	11.4	0.5	17	1	2.1	0.2
Mauritius	1	1	—	—	—	10.5	0.7	2	—	2.0	0.0
Total	1	12	7	—	—	11.3	0.6	19	1	2.1	0.2
<i>A. straussi</i>	—	15	33	9	1	11.9	0.7	36	22	2.4	0.5
Total scales in transverse series											
	13	14	15	16	17	18	$\bar{x}$	SD			
<i>A. kenyae</i>											
Kenya	7	7	4	—	1	—	14.0	1.1			
Mozambique	4	5	1	—	—	—	13.7	0.7			
Comoros	5	13	6	—	—	—	14.0	0.7			
Madagascar	2	1	1	—	—	—	13.8	1.0			
Total	18	26	12	—	1	—	13.9	0.8			
<i>A. mascarenensis</i>											
Réunion	—	11	6	1	—	—	14.4	0.6			
Mauritius	1	1	—	—	—	—	13.5	0.7			
Total	1	12	6	1	—	—	14.4	0.7			
<i>A. straussi</i>	—	12	22	19	4	1	15.3	0.9			

**Table 9** Frequency distributions of counts of predorsal and circumpeduncular scales for *Anisochromis* species.

	4	5	6	7	8	$\bar{x}$	SD	12	13	14	$\bar{x}$	SD
<i>A. kenyae</i>												
Kenya	—	1	5	3	1	6.4	0.8	9	1	—	12.1	0.3
Mozambique	1	1	1	1	—	5.5	1.3	3	2	—	12.4	0.5
Comoros	2	6	4	—	—	5.2	0.7	12	—	—	12.0	0.0
Madagascar	—	2	—	—	—	5.0	0.0	2	—	—	12.0	0.0
Total	3	10	10	4	1	5.6	1.0	26	3	—	12.1	0.3
<i>A. mascarenensis</i>												
Réunion	—	5	4	—	—	5.4	0.5	9	—	—	12.0	0.0
Mauritius	—	1	—	—	—	—	—	1	—	—	—	—
Total	—	6	4	—	—	5.4	0.5	10	—	—	12.0	0.0
<i>A. straussi</i>	5	13	11	1	—	5.3	0.8	21	8	1	12.3	0.5

**Table 10** Frequency distributions of position of first ctenoid scale (relative to anterior lateral line scales) for *Anisochromis* species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{x}$	SD
<i>A. kenyae</i>																
Kenya	—	1	7	5	—	—	—	—	—	—	—	—	—	—	3.3	0.6
Mozambique	2	1	3	2	—	—	—	—	—	—	—	—	—	—	2.6	1.2
Comoros	—	—	9	7	4	—	2	—	—	—	—	—	—	—	4.0	1.2
Madagascar	1	—	1	—	2	—	—	—	—	—	—	—	—	—	3.5	1.9
Total	3	2	20	14	6	—	2	—	—	—	—	—	—	—	3.6	1.2
<i>A. mascarenensis</i>																
Réunion	—	—	4	8	3	1	1	—	—	—	—	—	—	—	4.2	1.1
Mauritius	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Total	—	—	4	9	3	1	1	—	—	—	—	—	—	—	4.2	1.1
<i>A. straussi</i>	—	—	1	11	9	7	8	7	7	5	1	—	—	1	6.7	2.3

**Table 11** Frequency distributions of counts of posterior interorbital pores for *Anisochromis* species.

	<i>I</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	$\bar{x}$	<i>SD</i>
<i>A. kenyae</i>							
Kenya	—	3	5	2	—	2.9	0.7
Mozambique	—	4	—	1	—	2.4	0.9
Comoros	1	8	—	2	1	2.5	1.2
Madagascar	—	1	—	—	—	—	—
Total	1	16	5	5	1	2.6	1.0
<i>A. mascarenensis</i>							
Réunion	—	—	7	2	—	3.2	0.4
Mauritius	—	—	1	—	—	—	—
Total	—	—	8	2	—	3.2	0.4
<i>A. straussi</i>	4	25	—	—	—	1.9	0.4



**Aims and scope.** The Bulletin of the British Museum (Natural History) Zoology, was established specifically to accommodate manuscripts relevant to the Collections in the Department of Zoology. It provides an outlet for the publication of taxonomic papers which, because of their length, prove difficult to publish elsewhere. Preference is given to original contributions in English whose contents are based on the Collections, or the description of specimens which are being donated to enhance them. Acceptance of manuscripts is at the discretion of the Editor, on the understanding that they have not been submitted or published elsewhere and become the copyright of the Trustees of the Natural History Museum. All submissions will be reviewed by at least two referees.

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## CONTENTS

- 109 Type material of Stegocephalidae Dana, 1855 (Crustacea, Amphipoda) in the collections of The Natural History Museum, London, including the description of seven new species  
*J. Berge, W. Vader and A. Galan*
- 137 The genus *Ischioscia* Verhoeff, 1928 in Venezuela, with the description of six new species (Crustacea, Oniscidea, Philosciidae)  
*Andreas Leistikow*
- 169 A review of the genus *Erenna* Bedot, 1904 (Siphonophora, Physonectae)  
*P.R. Pugh*
- 183 A new species of loach, genus *Nemacheilus* (Osteichthyes, Balitoridae) from Aceh, Sumatra, Indonesia  
*R.K. Hadiaty and D.J. Siebert*
- 191 Revision of the western Indian Ocean fish subfamily Anisochrominae (Perciformes, Pseudochromidae)  
*A.C. Gill and R. Fricke*

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